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Marine Growth of Atlantic Salmon (*Salmo salar*) in the Northwest Atlantic

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ALLEN, K. R., R. L. SAUNDERS, AND P. F. ELSON. 1972. Marine growth of Atlantic salmon (*Salmo salar*) in the northwest Atlantic. J. Fish. Res. Bd. Canada 29: 1373–1380.

The fishery for Atlantic salmon in the west Greenland area has provided useful data for the study of marine growth of salmon. Length data from seaward migrating smolts, post-smolts, and 1-, 2-, and 3-sea-winter feeders taken at sea and 1-, 2-, and 3-sea-winter spawners taken by commercial fisheries, angling, and research traps, have been used to construct a tentative growth curve. Fish which spawned after 1 sea-winter (grilse) were smaller at the time of spawning than fish of the same smolt-class which had not matured but were still actively feeding at sea. Similarly, 2-sea-winter spawners were smaller than salmon which would not have returned until after a third sea winter. The growth rate of salmon during the summer prior to spawning was lower than that of fish which would have spawned a year or more later and appears to be about the same as that during the preceding winter.

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La pêche du saumon atlantique dans la région du Groenland occidental a permis de cueillir des données utiles sur sa croissance en mer. Une courbe provisoire a été établie à partir de mesures de longueur des stades suivants: smolts en route vers la mer, post-smolts, poissons ayant passé 1, 2 et 3 hivers en mer, encore au stade trophique et capturés en mer, ou sur le point de frayer et capturés par des engins de pêche commerciale, à la ligne ou dans des trappes expérimentales. Les saumons qui fraient après un hiver en mer (grilses) sont plus petits, au moment de la fraie, que ceux de la même classe, encore immatures et se nourrissant activement en mer. De façon semblable, les reproducteurs qui ont passé 2 hivers en mer sont plus petits que les poissons qui, normalement, n'auraient frayé qu'après un troisième hiver en mer. Le rythme de croissance des saumons durant l'été qui précède la fraie est plus lent que celui des saumons qui auraient frayé une ou plusieurs années plus tard, et semble être le même que celui de l'hiver précédent.

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UNTIL a substantial fishery was developed off the west coast of Greenland, Atlantic salmon from North American rivers were seldom caught in their marine phase between 3 months after their descent to sea and 6 months before spawning. As a result, little material other than that provided by scale reading was available for examining in detail the nature of growth during the marine phase. All that was known with any certainty was the size at which the fish went to sea, and the sizes at which they returned and spawned after different periods at sea. The development of the salmon fishery (Fig. 1) along the west coast of Greenland has provided material from this area and has stimulated additional research efforts to take salmon at sea.

In the Baltic Sea there has been an opportunity to study salmon during most of the period between entry as smolts and return as adults. Carlin (1963, 1964) has published data on the sizes of tagged Swedish salmon caught in the Baltic Sea at various ages. More recently, Thurow (1966) has published growth curves for salmon taken in the Baltic fishery between 1957 and 1963.

The present study draws together data on the size of Canadian Atlantic salmon at various stages during their marine life. These data are not sufficient for detailed comparisons of the growth of salmon originating in different areas or for consideration of year-to-year variations in growth of salmon of the same origin. They are, however, sufficient to enable preliminary growth curves to be drawn.

Data have been drawn primarily from the New Brunswick coast of the Gulf of St. Lawrence, particularly the Miramichi System, where research projects have been in progress for over 20 years (Henderson et al. MS 1965; Kerswill 1971; Saunders 1967, 1969; Schofield MS 1967). Other data have been drawn from the Bay of Fundy where smolts from the Pollett River have been caught after about 3 months in the sea. Data from fish of unknown origin captured on the high seas have also been used to fill gaps in the growth curves.

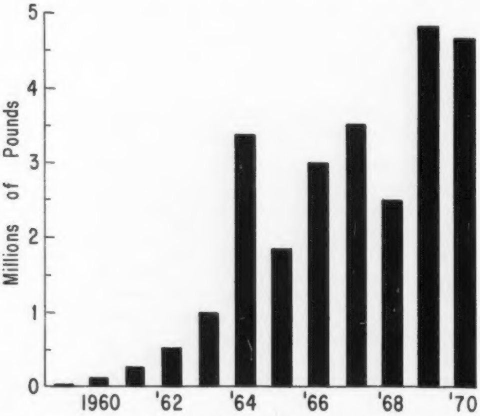

FIG. 1. Landings in the west Greenland salmon fishery, 1960–70. Figures for 1959–64 from Greenland inshore fishery; from 1965 onward figures include high seas catches in Davis Strait as well as inshore fishery. Data from ICNAF Comm. Doc. 71/14 (Anon. 1971).

Material

The principal data are summarized in Table 1, which shows the mean size and standard deviation of the length of fish taken as seaward migrating smolts and after various periods at sea up to returning spawners of 3 sea-winters. No fish returning for the first time after longer periods have been encountered during this study. The data are arranged approximately in order of increasing length of the marine life. Figure 2 shows locations of places named in Table 1.

The terminology used for the various life history stages is that of Allan (1965). The fish have been separated into "spawners" and "feeders." All "spawners" in this study were caught in or fairly close to rivers and at a time when most salmon in these fisheries showed no signs of feeding. "Feeders" were caught in distant marine areas and many had food in their stomachs. Considering the times and places of capture, some of these feeding fish would probably have spawned in the same calendar

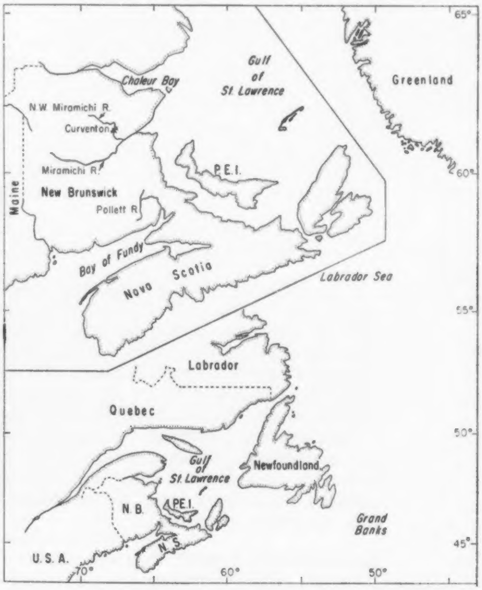

FIG. 2. Map of northwest Atlantic area, showing locations of places mentioned in text.

TABLE 1. Mean lengths (tip of snout to tip of relaxed tail fin), with mean dates of capture etc., of migrating smolts, salmon taken at sea, and returning adults used for study of marine growth rates of Atlantic salmon in the northwest Atlantic area.

Sample No.	Age-group	Origin	Mean date	Sample size	Mean length (*cm*)	Adjusted mean length[a] (*cm*)	Standard deviation (*cm*)	Coefficient of variation	Source of data
1	Smolt	Pollett R., N.B. (1952)	May 24	602	15.9	–	1.1	.07	Elson 1962, Table XIV
2	”	Northwest Miramichi R., N.B. (1965)	June 2	1000	14.7	–	–	–	Forsythe MS 1967
3	”	Northwest Miramichi R., N.B. (1966)	May 27	662	14.6	–	1.58	.11	Forsythe MS 1968
4	Post-smolt	Bay of Fundy (1952) (fin-clipped Pollett R.)	Aug. 15	61	28.8	–	2.19	.08	F.R.B.C. St. Andrews
5	Post-smolt	Bay of Fundy (1952–54) (mixed origin)	Aug. 16	325	29.7	–	2.19	.07	F.R.B.C. St. Andrews
6	1-sea-winter spawner (= grilse)	Northwest Miramichi R., N.B. (early run) (1963)	July 1	195	53.0	–	2.24	.04	Saunders and Allen 1967
7	”	Northwest Miramichi R., N.B. (late run) (1963)	Sept. 23	95	57.7	–	2.73	.05	Saunders and Allen 1967
8	”	Pollett R, N.B. (1953)	Oct. 26	69	59.8	–	3.85	.06	F.R.B.C. St. Andrews
9	1-sea-winter feeder	E. of Newfoundland (1966)	Aug. 15	4	51.2	53.8	–	–	W. Templeman (personal communication)
10	”	Labrador Sea and W. Greenland (1965)	Aug. 14	36	65.5	68.7	4.41	.07	W. Templeman (personal communication)
11	”	W. Greenland (1966) (tagged northwest Miramichi R.)	Oct. 10	48	64.6	66.0	3.23	.05	F.R.B.C. St. Andrews
12	2-sea-winter spawner	Miramichi R., N.B. and estuary (1954–66)	Aug. 29	1268	76.6	–	5.74	.08	F.R.B.C. St. Andrews
13	2-sea-winter feeder	E. of Newfoundland, Grand Banks (1966)	Apr. 7	36	68.9	72.3	4.16	.06	W. Templeman (personal communication)
14	2-sea-winter feeder	Labrador Sea and W. Greenland (1965)	July 27	2	83.1	87.3	–	–	”
15	3-sea-winter feeder	Labrador Sea (1966)	Mar. 23	1	87.4	91.8	–	–	”
16	3-sea-winter spawner	Gulf of St. Lawrence–N.B. coast (1954–66)	July 29	519	92.0	–	7.70	.09	F.R.B.C. St. Andrews

[a] Where fork length was originally recorded, values have been adjusted to length to tip of relaxed tail fin using the equation: length to tip of tail = 0.84 (*cm*) + 1.03 (*cm*) × fork length (*cm*) derived from measurement of 350 adult salmon taken at the Northwest Miramichi (Curventon) counting fence.

year; others would not have spawned until the next calendar year or later.

Sample No. 1 (Table 1) consists of naturally produced smolts trapped during their seaward migration in the Pollett River (data from Elson 1962).

Samples 2 and 3 are naturally produced smolts trapped in 2 successive years during their seaward migration in the Northwest Miramichi River (Fig. 2). The difference in the mean sizes of the two samples from this river is not significant. The Miramichi smolts were significantly smaller than those from the warmer Pollett River.

Samples 4 and 5 are of post-smolts taken in late summer in herring weirs along the southeast shore of the Bay of Fundy. Sample 4 consists of fin-clipped (adipose and both pelvics) fish taken during a single year and known to be of Pollett River origin, while sample 5 is composed of unmarked fish taken at the same time of year during 3 successive years.

The difference in size between samples 4 and 5 might have been owing to different stock origin, different growth rate between years or the effect of fin-clipping at the smolt stage which has been shown to reduce the size of returning grilse (Saunders and Allen 1967).

Samples 6 and 7 are data for grilse from a study of the effects of marking on Northwest Miramichi salmon (Saunders and Allen 1967). Because tagging at the smolt stage results in the returning grilse being significantly shorter than untagged fish (Saunders and Allen 1967), only untagged fish are used in samples 6 and 7. The average size of grilse increased during the season. Saunders (1967) has shown that there are distinct early (June–July) and late (September–October) runs in that river; few fish, usually, entered in August. The fish in both samples are regarded as being native to the river and the difference in mean size between fish of the two samples is assumed to represent their growth in the sea between June and September.

Sample 8 is composed mainly of unmarked grilse from the Pollett River, although it also includes 10 fin-clipped fish. The mean size of the fin-clipped fish was slightly greater than that of the unmarked fish, and Saunders and Allen (1967) found that fin-clipping caused less reduction in growth than tagging. There appears therefore to be no need to discard the fin-clipped fish as biassing the sample. The fish in sample 8 are regarded as being directly comparable with those in samples 1 and 5.

Samples 9, 10, 13, 14, and 15 are based on material collected by Dr W. Templeman of the St. John's Biological Station, Nfld., during experimental fishing operations between Newfoundland and Greenland. The unpublished information regarding these fish, which Dr Templeman has kindly allowed us to use, has assisted greatly in filling what would otherwise be major gaps in the growth picture.

Sample 11 consists of fish which were tagged as naturally produced smolts in the Northwest Miramichi River in 1965 and which were recaptured along the west coast of Greenland in the autumn of 1966.

Since the Miramichi fish recaptured in Greenland were all tagged, it is probable (Saunders and Allen 1967) that they also were slightly smaller than untagged fish from the same river. The ratio of the length of untagged to tagged grilse returning to the Miramichi in the early run was 1.019:1.000, and in the late run 1.028:1.000. The mean of these ratios is 1.024:1.000. Since it is likely that the adverse effect of tagging on growth rate occurs mainly in the first few weeks after tagging (Saunders and Allen 1967), it is assumed that tagged and untagged fish would have the same instantaneous growth rates during the later part of their marine life. Therefore, the ratio between their lengths is likely to be the same for fish returning as grilse and for those which remain at sea 1 or more years longer. The length of the tagged Miramichi fish taken in Greenland has been multiplied by 1.024 to obtain an estimate of the length of untagged fish at this stage.

Sample 12 consists of 2-sea-winter Miramichi fish caught in the freshwater reaches by angling or research operations, in nets and traps in the estuary or in driftnets off the mouth of the estuary. Examination of their scales verified that they had spent two winters at sea and had not spawned previously. About one-quarter of the fish in the sample were taken in the driftnet fishery off the Miramichi. Belding and Préfontaine (1938, 1939) found that this fishery takes, early in the season particularly, a large proportion of fish on their way to rivers further north in the Gulf of St. Lawrence. However, fish of Miramichi origin probably composed by far the majority of the sample. Allowing that nearly all of the salmon taken in Miramichi waters originated in that river and that half of those taken in the driftnet fishery were returning to the Miramichi, sample 16 gives a good estimate of the size of 2-sea-year Miramichi salmon.

Sample 16 consists of 3-sea-winter salmon spawning for the first time and taken from a variety of sources. To provide a large sample, fish taken anywhere along the Gulf of St. Lawrence coast of New Brunswick were included. Since much of the sample was taken in the driftnet fishery off the Miramichi, it is likely that many of the fish were not of Miramichi origin. Belding and Préfontaine (1938, 1939) found that even fewer of 3-sea-winter than of 2-sea-winter salmon from the Miramichi driftnet fishery were headed for the Miramichi. However, the driftnet fishery ends on August 15th so the late summer and autumn components of sample 16 were taken mostly from the Miramichi estuary and river. Sample 16 may be taken as indicative of the size of 3-sea-winter Miramichi salmon.

Data are also available on the growth made by salmon which were tagged as grilse at the Curventon counting fence (Fig. 1) and subsequently recaptured (Table 2). The fish have been divided into two groups, those captured after approximately 1 year in the sea and those after approximately 2 years. There is no important difference between these two groups in regard to either date or size at marking. Their mean size at marking was intermediate between that of the early- and late-running grilse in samples 6 and 7 and does not differ significantly from the mean for samples 6 and 7 combined.

Results and Discussion

The mean lengths in Table 1 are plotted in Fig. 3, except samples 1 and 2 which are overlapped

TABLE 2. Growth rates, as shown by mean total lengths (tip of snout to tip of relaxed tail fin), of fish which spawned as grilse and spent 1 or 2 additional years at sea.

		Mean date			Mean length			Mean growth rate	
Years absence	No. of fish	Marking	Return	Interval (*days*)	Marking (*cm*)	Return (*cm*)	Increment (*cm*)	Linear (*cm/day*)	Instantaneous (*monthly*)
1	19	Aug. 1	June 22	325	54.4	63.5	9.1	.028	.0142
2	12	Aug. 4	June 18	683	54.1	77.4	23.3	.034	.0157

by 3, and sample 4 which is overlapped by 5. The range of one standard deviation on each side of the mean is shown for the point representing each sample mean except for samples 9, 14, and 15 which are too small to warrant such treatment. A progressive falling off in growth rate is indicated. To provide a suitable envelope curve to describe the maximum mean size at any age, a von Bertalanffy curve has been fitted to the points corresponding to samples 3, 5, 10, 11, 14, 15, and 16, using the method of Allen (1966). The points were weighted according to the size of the samples but variation within the samples was not taken into account. The resulting curve is given by

$$L = 99.06\,(1-e^{-.0642[t-2.313]})$$

and is represented by the solid line on the figure.

It is evident that while this curve passes close to most of the points for fish taken during the ocean feeding stage, the points for fish which have entered rivers or have been taken by inshore fisheries are consistently below it. This applies to points 6, 7, and 8 for grilse returning to the Northwest Mira-

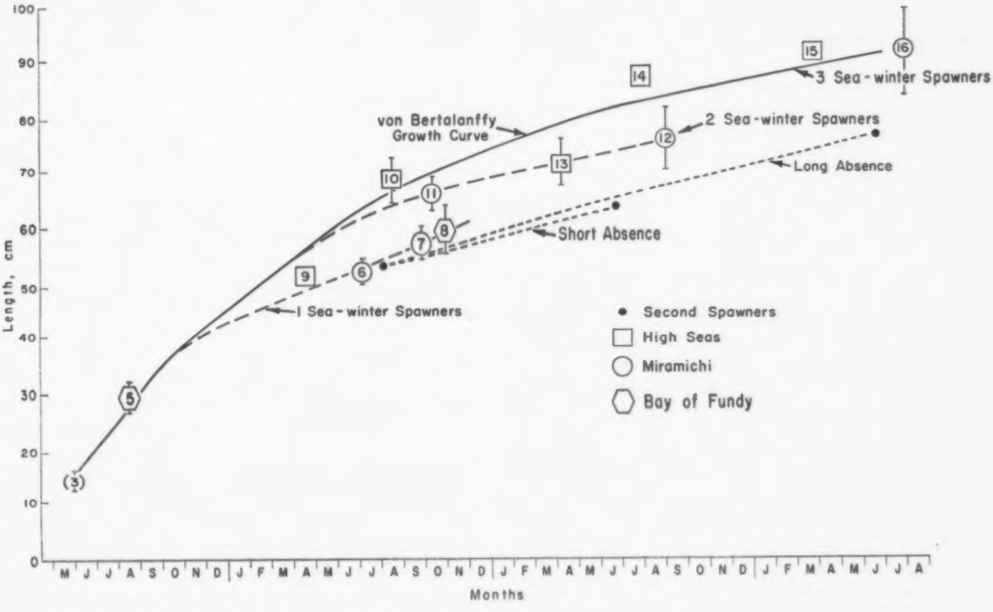

FIG. 3. Growth curves of Northwest Atlantic salmon, based on samples in Table 1. Solid line, von Bertalanffy envelope curve fitted to points representing migrating smolts and fish in the actively growing marine phase; broken lines, curves applying to fish which have passed through most or all of their last sea-winter preceding first sexual maturity; dotted lines, growth curves for fish which matured first as grilse but have survived to approach a second maturity after 1 or 2 more years at sea.

michi and Pollett rivers and point 12 for 2-sea-winter spawners returning to the Miramichi area. The 3 grilse points fit closely to a line which may be extrapolated backwards to reach the von Bertalanffy curve sometime during the preceding winter. Point 9, based on only four fish, lies slightly above the grilse line through points 6, 7, and 8.

If a line with a slope similar to that for grilse is drawn through point 12, it will also pass through point 11. Point 11, which is for Northwest Miramichi tagged fish taken in Greenland, probably represents potential 2-sea-winter fish which on return would correspond with point 12 since they (point 11) did not mature as grilse. Among the large salmon returning to the Miramichi, 2-sea-winter fish greatly outnumber 3-sea-winter fish. For example, a sample of 969 salmon returning to the Miramichi River for the first time after more than one winter in the sea contained only 43 3-sea-winter fish, the remainder being 2-sea-winter fish. While it is not known whether most Miramichi salmon which go to Greenland would return as 2-sea-winter fish, point 11 is regarded as representing the size of potential 2-sea-winter spawners while in Greenland waters. Therefore, the line connecting these points represents approximately the growth of 2-sea-winter Miramichi fish over their last year at sea. Point 13 lies almost exactly on this line. These fish were taken in the south Labrador Sea and northwest Atlantic, generally 200–350 miles from the Newfoundland coast. It is assumed that they were potential 2-sea-winter spawners.

The Miramichi fish taken on the Greenland coast (point 11) were taken very little later than those returning to the river as late-run grilse (point 7) and they are much larger. Thus, of fish originating in the same river and from the same smolt class, those which mature after 1 sea-winter grow more slowly during the spring and summer immediately preceding their return to the river than do those which do not return until they have spent 2 or more years at sea.

The data also suggest that a similar relation exists between fish returning after 2 sea-winters and after 3 sea-winters. Point 11 lies well below a smooth von Bertalanffy curve leading past points 14 and 15, up to point 16. Points 14 and 15 represent very few fish but they are well outside the normal range for 2-sea-winter spawners and are consistent with the larger sample represented by point 16.

The fish in sample 10 were a little larger ($P < 0.01$) than those in sample 11, even though they were caught earlier in the year. They were taken by experimental driftnet fishing in the same general area as those of sample 11, mostly fairly close to the Greenland coast. Returns from tagged fish have

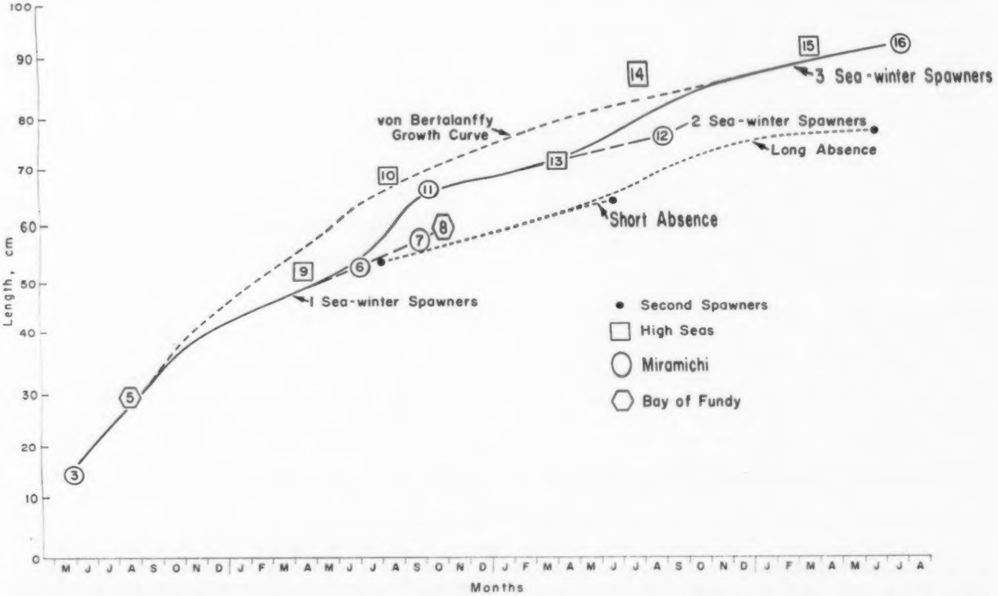

FIG. 4. Growth curves based on von Bertalanffy envelope curve of Fig. 2 but modified to conform with recognized patterns of seasonal growth rates for salmon.

shown that salmon caught along the Greenland coast originate from both sides of the Atlantic (Saunders et al. 1965; Anon. 1971). The Northwest Miramichi River, whose contributions to various fisheries have been studied in detail, contributes many salmon to the Greenland fishery (Saunders 1969). However, sample 10 appears to include faster growing fish than the bulk of Miramichi stock (compare with samples 11 and 12). It may also include a larger proportion of fish which would have spent three winters in the sea before returning.

Figure 3 also shows the growth made by fish which first spawned as grilse and returned a second time after 1 or 2 additional years at sea (Table 2). The rate of growth for those spending 2 additional years in the sea appears to be slightly greater than for those spending 1 additional year in the sea. The rate of growth of those returning after 1 additional year appears to be almost identical with that of 2-sea-winter spawners during their second year in the sea; that of fish returning after 2 additional years parallels closely the growth of 3-sea-winter spawners. It appears, therefore, that fish spawning for a second time grow, in intervals between spawnings, at about the same rate as fish of the same age which have not previously spawned.

The foregoing discussion is based on the assumption that growth proceeds without seasonal fluctuations. This assumption is not consistent with the accepted basis for determining age and growth of salmon during both stream and marine phases, namely that the wide and narrow bands of scale circuli indicate periods of rapid and slow growth, respectively. This technique assumes that in each year the salmon pass through a period of rapid "summer" growth marked by the appearance of widely spaced circuli on the scales, and a period of slow "winter" growth marked by a band of closely spaced circuli. That such seasonal alternation of growth rate does occur during the freshwater life of salmon has been shown (Allen 1940, 1941). He found that parr growth in British rivers practically ceased when temperature fell below 7 C.

The temperatures experienced by marine salmon at any season depend upon where they were living. W. Templeman (personal communication) caught the salmon included in samples 10, 14, and 16 in July and August in water of surface temperatures between 2.3 and 9.6 C, and those in samples 9, 13, and 15 in March and April in water of surface temperatures between 3.7 and 6.1 C. The fish, at least in the July–August samples, had been feeding freely. Hence, feeding and probably also growth take place at lower temperatures in the sea than in fresh water. In Fig. 4 curves below the von Bertalanffy envelope curve have been fitted by inspection to the same points used in Fig. 3 on the four hypotheses: (a) that growth is seasonal, (b) that the period of rapid growth is generally between April and November, (c) that some growth takes place, although at a slower rate, during the remainder of the year, and (d) that fish which are maturing continue to grow during the summer at about the same rate as during the preceding winter.

TABLE 3. Comparison of seasonal growth rates of Baltic salmon (summarized from Thurow 1966, Table 44) and northwest Atlantic salmon (Fig. 4), as shown by mean total length (tip of snout to tip of relaxed tail fin) of salmon caught in different months.

Sea winters	Month	Baltic (*cm*)	Northwest Atlantic (*cm*)
1	Jan.	47.9	42.5
	Apr.	52.8	48.2
	Nov.	72.4	66.0
2	Jan.	74.8	68.6
	Apr.	75.2	73.0
	Nov.	92.2	88.2
3	Jan.	94.4	90.2
	Apr.	95.6	91.8
	Nov.	–	–

Data from the Baltic Sea (Thurow 1966) indicate that growth there is much slower in winter than in summer. Table 3 compares the mean length of Baltic (data summarized from Thurow's Table 44) and Northwest Atlantic salmon (from Fig. 4) at several times during their marine life. The Northwest Atlantic data are for fish which would not have spawned in the year of capture. They were, therefore, probably growing more rapidly than the average for a composite population of feeders and spawners such as Thurow used. It appears that the winter reduction of growth rate is not as severe in the northwest Atlantic as it is in the Baltic. But summer growth is more rapid in the Baltic than in the northwest Atlantic. Thurow makes no distinction between fish which are maturing and those which will continue to feed for another year. It is apparent that Baltic salmon are larger at a given age than those from the northwest Atlantic.

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Biology of *Bothrimonus* (= *Diplocotyle*) (Pseudophyllidea: Cestoda): Ecology, Life Cycle, and Evolution; a Review and Synthesis[1]

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SANDEMAN, I. M., AND M. D. B. BURT. 1972. Biology of *Bothrimonus* (= *Diplocotyle*) (Pseudophyllidea: Cestoda): ecology, life cycle, and evolution; a review and synthesis. J. Fish. Res. Bd. Canada 29: 1381–1395.

An integrated account of the ecology and life cycle of *Bothrimonus* is synthesized from the literature, experiment, and observation of larval and adult stages of the parasite. *Bothrimonus* has a circumpolar distribution in boreal or subarctic conditions. As an adult it is found in a wide variety of fish hosts which feed in littoral or estuarine waters. Adult worms have a short life-span in the fish host and occur only seasonally. A single intermediate host appears to be involved in the life cycle and this is most commonly a brackish-water gammarid. The operculate eggs, which contain unciliated larvae, possess characteristic polar filaments which have an adhesive function. Entry is almost certainly by ingestion of eggs by the gammarid host; the larval forms often attain sexual maturity within the gammarid host with accompanying production of apparently normal eggs. Although it has been possible to infect fish hosts experimentally with larval stages, it has not yet been possible to infect gammarids with eggs obtained either from neotenic individuals in gammarids or from adults in the fish host.

The life cycle of *Bothrimonus* indicates closer affinities of the Cyathocephalidae with caryophyllaeid than with other pseudophyllidean tapeworms. Distribution is discussed in terms of its evolution and a freshwater origin in the Ponto–Aralo–Caspian province is proposed.

SANDEMAN, I. M., AND M. D. B. BURT. 1972. Biology of *Bothrimonus* (= *Diplocotyle*) (Pseudophyllidea: Cestoda): ecology, life cycle, and evolution; a review and synthesis. J. Fish. Res. Bd. Canada 29: 1381–1395.

Les auteurs présentent une synthèse de l'écologie et du cycle évolutif de *Bothrimonus* à partir de travaux publiés sur le sujet, d'essais en laboratoire et d'observations des stades larvaires et adultes du parasite. *Bothrimonus* a une aire de répartition circumpolaire dans l'empire boréal ou subarctique. Au stade adulte, on le trouve chez une grande variété de poissons qui se nourrissent près des côtes ou dans les estuaires. La durée de vie de l'adulte dans le poisson hôte est brève, et son occurrence n'est que saisonnière. Il ne semble y avoir qu'un seul hôte intermédiaire, le plus souvent un gammaride d'eau saumâtre. L'oeuf operculé, renfermant une larve dépourvue de cils, est muni de filaments polaires adhésifs caractéristiques. Il est presque certain que le parasite pénètre dans le gammaride hôte par ingestion des oeufs, la forme larvaire atteignant souvent la maturité sexuelle dans cet hôte, et y produisant des oeufs apparemment normaux. Quoique on ait pu introduire expérimentalement des larves de parasite dans des poissons, il a été impossible jusqu'ici d'infecter des gammarides avec des oeufs provenant de néoténiques parasites de gammarides ou d'adultes prélevés dans des poissons.

Le cycle évolutif de *Bothrimonus* démontre que les Cyathocephalidae sont plus étroitement apparentés aux caryophylléides qu'aux autres vers plats pseudophyllidiens. Les auteurs discutent de la répartition du genre en termes de son évolution, et suggèrent une origine dans les eaux douces de la région ponto–aralo–caspienne.

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[1] This is the second of two papers on the biology of *Bothrimonus*. The first appeared in this Journal, Vol. 26, No. 4, 1969.

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BOTHRIMONUS (= *Diplocotyle*) is an interesting tapeworm partly because of a life cycle which includes progenesis in its intermediate invertebrate host, a gammarid, and partly because of its primitive evolutionary status. The possession of multiple reproductive organs coupled with the lack of segmentation places *Bothrimonus*, together with *Spathebothrium* and *Cyathocephalus*, somewhere between the caryophyllaeid and other pseudophyllidean tapeworms. The life cycle of *Cyathocephalus* is fairly well known through the work of Wisniewski (1932, 1933), but nothing is known of the biology of *Spathebothrium*. Although there is no experimentally based information on *Bothrimonus*, there is a considerable body of observation and speculation widely scattered through the literature. In this study the authors review current fact and theory concerning the ecology, life cycle, and evolution of *Bothrimonus*, present new information from observation and experiment, and propose a coherent view of these aspects of its biology.

Stages in the Vertebrate Host

As indicated in the historical review of the taxonomy of *Bothrimonus* in an earlier work (Burt and Sandeman 1969) it had been common practice to ascribe material to one or other of several genera (and species) depending on the fish host involved. The reduction of all material previously ascribed to *Diplocotyle*, *Didymobothrium*, and *Bothrimonus* to the single (polytypic) species *Bothrimonus sturionis* renders unnecessary any further addition to the already considerable discussion in the literature of what constitutes the "normal" or "preferred" host.

The outstanding feature that the fish hosts (Table 1) have in common is that they are marine for at least part of their life cycle and feed in the littoral or sublittoral zones of the shore or under estuarine conditions. There are some apparent exceptions; for example, Wardle (1932) recorded *D. olrikii* from the two freshwater species *Leucicthys artedi* and *Coregonus clupeaformis* in the Canadian arctic. There is, however, some evidence that these species run regularly down to salt water in the area concerned (Dymond 1933). Similarly, with respect to the two records from normally deepwater marine fish, *Gymnacanthus tricuspis* and *Anarhichas lupus*, Polyanskii (1955) observed that, from the presence of the parasites *Podocotyle atomon* and *Prosorhynchus squamatus*, *Gymnacanthus tricuspis* must sometimes approach the coast. He also observed that on several occasions the species was caught near the littoral zone. In the case of *A. lupus*, Polyanskii (1955) reported that the single parasitized fingerling was caught close to the coast.

In addition to the taxonomic difficulties raised by Duvernoy's (1842) description, his host and locality records are also problematical. Duvernoy (1842), in referring to *B. sturionis*, stated that "(il) a été découvert, en 1835, par M. Lesueur dans le canal intestinal d'un Esturgeon (l'*Acipenser oxyrhynchus* Mitschil (sic)), pris non loin de l'embouchure, dans l'Ohio, de la rivière de Wabash qui arrose l'Indiana...." Although access to the Wabash River from the Gulf of St. Lawrence or the Gulf of Mexico, in both of which the Atlantic sturgeon is present, by the Welland Canal or the Mississippi and Ohio rivers might be possible (but unlikely because of the distances involved), there is no record, as far as we are aware, either by LeSueur or by any other author, of this species of sturgeon occurring in this particular region. On the other hand, it seems improbable that LeSueur could have mistaken the identity of the host. It seems more likely to us that LeSueur's identification was correct but that a label with such information as the locality may have been somehow transposed.

SEASONAL OCCURRENCE AND LONGEVITY

The dated records (Table 1 and Fig. 1) of *Bothrimonus* indicate a seasonal occurrence. Records from the arctic and subarctic (Schneider 1902a, 1902b, 1903; Cooper 1921; Nybelin 1922; Guiart 1935; Wardle 1932; and present paper) fall within the months June–December with the majority in the June–August period. From eastern North America the records run between April and May for the more northerly, eastern Canadian material (Heller 1949) and our own material. The single dated record for the Mediterranean, by Rudolphi (1819), is for July, and Nybelin's (1922) records for the Caspian Sea are for April. These records indicate a seasonal occurrence which varies for the geographic area and latitude with, as one might expect, the more temperate regions generally yielding the earlier records. We believe that these records, limited as they are because many authors did not give the date of collection or report negative results, represent more than just a reflection of the fact that most collecting is done in the summer months. Linton's (1941) paper is particularly helpful as his reports are based on collections "made in each month of the year for many years" and he found the parasite only in April and May. In Passamaquoddy Bay, N.B., although we found an infection rate of 30% in June, no parasites were recovered from winter flounders examined in November.

A stricter analysis of the dated records would be a formidable task because the temperature and other physical conditions in any locality vary from year to year, and long term climatic changes also complicate the picture. The physical conditions play a large role in determining if and when hosts are parasitized both by affecting the development of the parasite in the gammarid host and by affecting the movements and feeding behavior of the fish hosts. The records for Iceland are a case in point: the considerable differences between the records for the north coast (September–December) and the south coast (April–July) can be explained by the considerable differences in the hydrology and climates of the

TABLE 1. Hosts, localities, and dates of collection of original records of *Bothrimonus*.

	Source	Name	Host	Locality	Date of collection
(1)	Fabricius (1780)	*Bothriocephalus punctatus* (Rud.)	*Salmo carpio* (= *Salvelinus alpinus* according to Zhukov 1963)	Greenland	
(2)	Rudolphi (1819) (in Monticelli (1890))		*Pleuronectes solea* (= Solea vulgaris)	Naples	July
(3)	Duvernoy (1842)	*Bothrimonus sturionis* Duv.	*Acipenser oxyrhynchus*	Wabash R. Ohio	
(4)	Krabbe (1874)	*Diplocotyle olrikii* Kr.	*Salmo carpio* (= *Salvelinus alpinus* according to Zhukov 1963)	Greenland	
(5)	Zchokke (1887)		*Solea impar* *Solea vulgaris*	Gulf of Naples	
(6)	Monticelli (1890)	*Diplocotyle rudolphi* Montic.	*Solea impar*	Bay of Naples	
		Diplocotyle olrikii Kr. (specimens from British museum)	*Salmo sp.*	Kara Sea	
(7)	Riggenbach (1898, 1899)	*Cyathocephalus catinatus*	*Solea vulgaris*		
(8)	Jaquet (1899)	*Bothriocephalus punctatus* Rud. redescribed as *Bothrimonus fallax* Lühe, 1900	*Acipenser ruthenus*	Rumania	
(9)	Schneider (1902a, b)	*Bothrimonus nylandica* Schn.	*Pleuronectes flesus*	Gulf of Finland	June 27, 1900
(10)	Schneider (1903)	*Bothrimonus nylandica* Schn.	*Pleuronectes flesus*	Gulf of Finland	June 17
(11)	von Linstow (1903)	*Diplocotyle cohaerens* v. Linst.	*Pleuronectes flesus*	Murman Coast	
(12)	Cholodkovsky (1914 1915)	*Bothrimonus caspicus* Chol.	*Acipenser guldenstadti*	Caspian Sea	
(13)	Cooper (1917, 1918)	*Bothrimonus intermedius* Cooper	*Pseudopleuronectes americanus* *Microgadus tomcod*	Brandy Cove, St. Croix R., N.B.	
(14)	Cooper (1921)	*Bothrimonus intermedius* Cooper	*Salvelinus malma*	Collinson Point, Alaska	July 8, 1914
				Cockburn Point, Bernard Harbour, Northwest Territories	Aug. 30, 1914 Sept. 6, 1914 End Aug., 1915
			Coregonus sp.	Marsh R. Collinson Pt.	July 12, 1914
			Zoarces anguillaris	St. Andrews, N.B.	July, Aug. 1919
(15)	Nybelin (1922)	*Diplocotyle olrikii* Kr.	*Salmo alpinus*	Greenland, Godhavn Iceland, Ofjord, Iceland, Hornefjord	June 20, 1901
			Artediellus uncinatus	Greenland, Mackenzie Bay	July 13, 1900
		Diplocotyle nylandica Schn.	*Pleuronectes limanda*	Iceland, Bernfjord	Dec. 10, 1901
				Iceland, Snertastadir	Sept. 26, 1903
			Pleuronectes platessa	Iceland, Adalvik	June 3, 1892
			free-living	Spitzbergen, Eisfjord	July 21, 1908
			Cottus scorpius	Iceland, Seydisfjord	May 23, 1903

(*Continued*)

TABLE 1. Hosts, localities, and dates of collection of original records of *Bothrimonus*. — (*Concluded*)

	Source	Name	Host	Locality	Date of collection
		Bothrimonus fallax Lühe	*Acipenser stellatus*	Russia, Astrachan Transcaspian, Kulali	Apr. 11, 13, 1899 Apr. 22, 1899 May 22, 1899
(16)	Bazikalova (1932)	*Diplocotyle cohaerens* v. Linst.	*Pleuronectes platessa*	Murman Coast	
(17)	Wardle (1932)	*Diplocotyle olrikii* Kr.	*Salvelinus alpinus stagnalis*	Hudson Bay, Wakeham Bay, Ungava, Churchill R.	
			Salvelinus fontinalis	James Bay, Wakeham Bay, Sugluk Strait	
			Leucichthys artedi	James Bay, Churchill R.	
			Coregonus clupeaformis	Hudson Bay, Churchill R.	
			Myoxocephalus quadricornis	Wakeham Bay	
(18)	Guiart (1935)	*Diplocotyle olrikii* Kr.	*Salvelinus salvelinus*	West Spitzbergen, baie Advent, Icefjord	Aug. 11–12, 1898
(19)	Dogiel and Markov (1937)	*Diplocotyle olrikii* Kr.	*Salvelinus alpinus*	Novaya Zemlya Bezimyannoi Gulf, Brandta Bay, Nechvatova River	June, July Aug. Aug.
(20)	Dogiel and Bychowsky (1938)	*Bothrimonus fallax* Lühe		Caspian Sea, Os. Sara Os. Chechen	
(21)	Linton (1941)	*Bothrimonus intermedius* Cooper	*Acanthocottus octodecimspinosus*	Woods Hole	Apr. 21, 1916
			Microgadus tomcod	Woods Hole	Apr. in 3 years
			Morone americana	Woods Hole	Apr. & May
			Tautoga onitis	Woods Hole	Apr.
(22)	Bauer (1941)	*Diplocotyle olrikii* Kr.		Khatanga R.	
(23)	Petrushevskii, Mosevich and Shchupakov (1948)	*Diplocotyle olrikii* Kr.	*Coregonus autumnalis*	Obskaya Guba, Se-Yakha	
		Diplocotyle nylandica (Schn.)	*Liopsetta glacialis knipowitschi*	Obskaya Guba	
(24)	Bauer (1948a)	*Diplocotyle olrikii* Kr.	*Coregonus autumnalis*	Yeniseyskiy Zaliv	
(25)	Bauer (1948b)	*Diplocotyle olrikii* Kr.	*Coregonus sardinella*	Laptev Sea, Tiksi Bay	Aug.
			Coregonus autumnalis	Laptev Sea, Tiksi Bay	Aug.
			Coregonus lavaretus pidschian n. *brachymystax*	Laptev Sea, Tiksi Bay	Aug.
			Coregonus muksun	Laptev Sea, Tiksi Bay	Aug.
		Diplocotyle nylandica (Schn.)		Laptev Sea, Tiksi Bay	Aug.
(26)	Heller (1949)	*Diplocotyle olrikii* Kr.	*Pseudopleuronectes americanus*	Baie de Chaleur	June 28
(27)	Shulman & Shulman–Albova (1953)	*Diplocotyle nylandica* (Schn.)	*Pleuronectes flesus bogdanovi*	White Sea, Onezhskaya Zaliv	
(28)	Polyansky (1955)	*Diplocotyle nylandica* (Schn.)	*Pleuronectes flesus* *Gymnacanthus tricuspis* *Anarhichas lupus*	Barents Sea	

(29)	Ronald (1958)	*Diplocotyle olrikii* Kr.	*Hippoglossoides platessoides*	St. Mary's Bay, N.S.	
			Limanda ferruginea		
			Pseudopleuronectes americana	St. Mary's Bay, N.S., and Passamaquoddy Bay, N.B.	
(30)	Mamaev et al. (1959)	*Diplocotyle olrikii* Kr.	*Oncorhynchus masu*	Datta	
			Salvelinus malma	Datta	
			Salvelinus leucomaensis	Icha (Kamchatka)	
(31)	Zhukov (1960)	*Diplocotyle* sp.	*Salvelinus leucomaensis*	Shikotan Is.	
(32)	Trofimenko (1962)	*Diplocotyle* sp.	*Salvelinus leucomaensis*	Kamchatka, Penzhina R.	
(33)	Martyanova–Glebova (1962)	*Diplocotyle olrikii* Kr.	*Salvelinus leucomaensis*	Bolshaya Iska R.	
(34)	Margolis (1963)	*Diplocotyle olrikii* Kr.	*Oncorhynchus nerka*	Kodiak Is., Karluk R.	
				Kodiak Is., Chignik R.	
(35)	Zhukov (1963)	*Diplocotyle olrikii* Kr.	*Salvelinus malma*	Chukotsk Peninsula, Lavrentiya Bay, and Provideniya Bay	
			Gadus morhua macrocephalus		
			Eleginus gracilis		
			Pholis dolichogaster		
			Hexagrammos stelleri		
			Melletes papilio		
			Myoxocephalus polyacanthocephalus		
			Myoxocephalus axillaris		
			Myoxocephalus platicephalus		
			Enophrys diceraus		
			Blepsias bilobus		
			Podothecus acipenserinus		
			Liparis gibbus		
			Platessa quadrituberculata		
			Pleuronectes stellatus		
(36)	Burt & Sandeman (1969)	*Bothrimonus sturionis* Duv.	*Pseudopleuronectes americanus*	St. Andrews, N.B.	June
			Microgadus tomcod	Woods Hole, Mass.	
			Salmo salar	Newfoundland, Terra Nova R.	June 8–10
			Apeltes quadracus	Newfoundland, St. Mary's Bay	June
			Oncorhynchus gorbuscha	Attu Is.	
			Salvelinus alpinus	Greenland	
(37)	Dogiel & Volkova (1946)	*Diplocotyle* sp.	*Gammarus locusta*	Kharlovsk	
(38)	Ouspenskaia (1960)	*Diplocotyle* sp.	*Anonyx nugax*	Murmansk Coast	
(39)	Sudarikov & Kurochkin (1964)	*Bothrimonus fallax* Lühe	*Dikerogammarus haemobaphes*	Caspian Sea, Mangishlak Peninsula	
(40)	Stark (1965)	*Diplocotyle* sp.	*Gammarus zaddachi zaddachi*	Esk R. Estuary	Dec.–Apr.
(41)	Sandeman (1962), Burt (1967), Burt & Sandeman (1969)	*Bothrimonus sturionis* Duv.	*Marinogammarus finmarchicus*	St. Andrews, Scotland	Feb.–May
			Marinogammarus pirlotti	St. Andrews, Scotland	Feb.–May
			Gammarus oceanicus	Newfoundland, Witless Bay	June 26, 1964
				Newfoundland, Green's Harbour	May 27, 1964

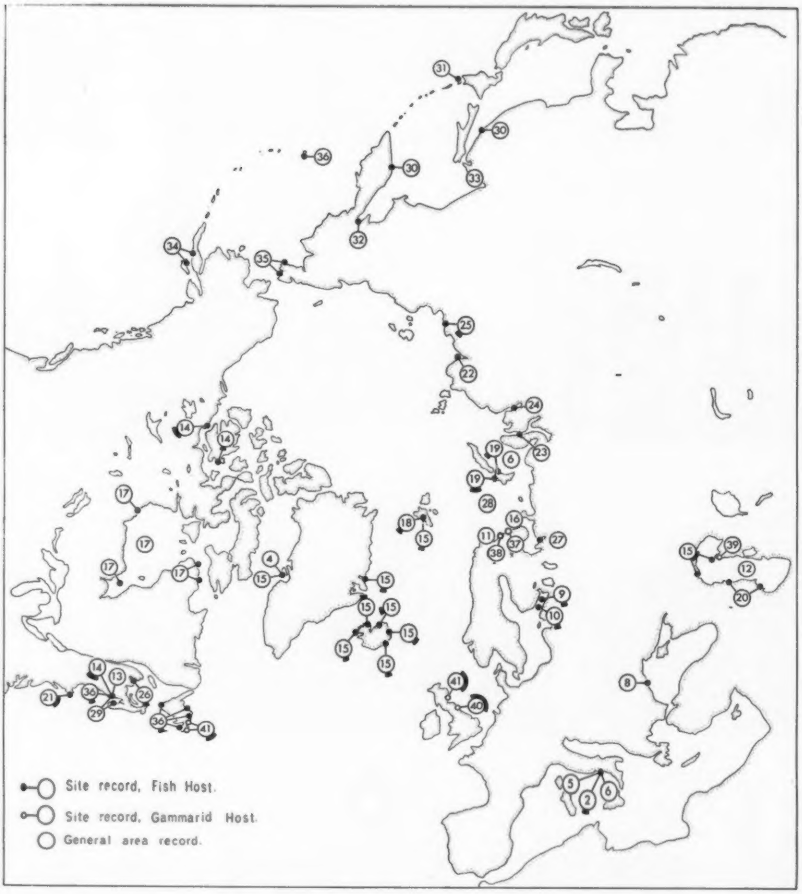


FIG. 1. Distribution of *Bothrimonus*. Numerals within the circles refer to the authors (see Table 1). The month of each record, where reported, is indicated by the clockwise sequence of the dark segments surrounding each circle.

two regions. However, it should be noted that, according to Zenkevitch (1963), these differences in hydrology have largely disappeared in recent years.

From this seasonal occurrence one can deduce that the parasite is short-lived in the fish host. Bauer (1948b) and Petrushevskii and Bauer (1948) reported it in the intestines of fishes from the Bay of Tiksi at the mouth of the Lena River and that it was absent from fish at Titari. The absence of the parasite from fish taken in fresh water was attributed by these authors to the parasite's inability to survive transportation into fresh water. Zhukov (1963) reported a similar phenomenon in *Salvelinus malma* in far eastern USSR waters and accepted Bauer's explanation. Mamaev and Oshmarin (1963), on the other hand, attributed the limited distribution of the parasite to its short life-span and noted the progenetic development in the invertebrate host reported by Dogiel and Volkova (1946). We agree with this view of Mamaev and Oshmarin. The seasonal occurrence and limited distribution can only be explained if the parasite is short-lived in its fish host. However, the exact length of time spent in the fish host is not known and may vary from one host to another. Our worms obtained from salmon smolts were in some cases immature and folded in the manner in which they are typically found in the hemocoel of the gammarid host and had probably been introduced within hours. On the other hand, the worms we found in flat fish were much larger and fleshier and active. There is no clear record of *Bothrimonus* in a fish taken far from the coast that might give a hint at the length of time involved and experiments (reported elsewhere in this paper) which might have shed some light on this point were inconclusive.

DISTRIBUTION

Zhukov (1963) dealt at some length with the distribution of *Bothrimonus*. He noted particularly the arctic circumpolar nature of the species which he related to the limits of drift ice and the presence of cold-water currents. He was either not aware of or ignored some of the more southerly records such as those from Wood's Hole and the Mediterranean. Earlier, Polyanskii (1955) listed *D. nylandica* among the lower arctic fauna of the Barents Sea and *D. olrikii* as arcto-boreal. The present more complete distribution map (Fig. 1) confirms the circumpolar distribution of the parasite but indicates that it should be ascribed to the subarctic and boreal zones with only occasional occurrences in the high arctic. However, as the species appears to be predominately estuarine, the allocation to particular marine zones should only be undertaken with some reservations. Without the support of experimental evidence we would not support Zhukov's (1963) suggestion that temperatures below 0 C are necessary for the normal development of the species.

Bothrimonus has commonly been referred to as a "marine" or "littoral" parasite; for example, by Bauer and Shulman (1948), Petrushevskii and Bauer (1948), Polyanskii (1955), and, by implication, Zhukov (1963). Other authors, notably Mamaev et al. (1959) and Mamaev and Oshmarin (1963), have referred to it as an estuarine species. Unfortunately, most records do not give information on the exact sites at which parasitized fish were caught, but the preponderance of records from bays, inlets, river mouths, and the lower stretches of rivers leads us to the conclusion that the species is more commonly littoral–estuarine than littoral–marine; this is confirmed by what is known of the intermediate host.

Stages in the Invertebrate Host

Our first larval material was collected in St. Andrews, Scotland, in *Marinogammarus finmarchicus* between February and May of 1956 from a series of shallow tide pools at the foot of a cliff where the water, at least at low tide, was diluted by seepage from the cliffs. In later years further material was obtained from *Marinogammarus pirloti* Sexton and Spooner from a different area of the shore, this time from under stones in the bed of a trickle of fresh water which was covered at high tide. Again parasitized gammarids were found only between February and April. Our Newfoundland material which was all of gravid worms, was collected and kindly donated by Dr D. H. Steele of Memorial University from the shorelines of Witless Bay and Green's Harbour. Although collections were made over the course of many months, parasitized specimens of *Gammarus oceanicus* were found only in late May and in June.

Of our Scottish material collected in 1956, the worms collected in late February and early March were small (7–35 mm), immature, and with a strobila much thinner than the scolex. The specimens collected in late March were not significantly smaller than those collected in April and May but 27% of the former were not gravid while all of the latter material was gravid. In March and April of 1964 all the worms recovered were gravid and of two worms collected in mid-February of 1966 one was gravid while the other was small (15 mm) and immature.

Infected gammarids lack pigmentation to the extent that the outline of the larvae could be distinguished through the body wall of the host (Fig. 2). In most living parasitized gammarids, brown clumps of eggs within the uteri of the worms could also be distinguished. As well as being easily recognized, parasitized individuals were sluggish and easily caught. Although individuals usually harbored single plerocercoids, two, or even three, were not uncommon. The bulk of the parasite is relatively large in relation to the bulk of the host (Fig. 3), the worms lying folded within the ventral hemocoel of the host, and there is considerable displacement of the body organs (Fig. 4). In one sectioned gammarid, eggs were present free in the hemocoel (Fig. 4). When worms from either a gammarid or fish host were placed in sea water, or diluted sea water, eggs were immediately extruded from the uterus. About 10% of these eggs contained oncosphere hooks.

Records of *Bothrimonus* in its gammarid host (Table 1, Fig. 1) are relatively few in number and more information on this phase of the life cycle, such as that provided by Stark (1965), would be invaluable. The gammarids involved are, for the most part, euryhaline brackish-water species from the littoral zone of shore or estuaries. An exception appears to be *Anonyx nugax* reported from the "Zone cotière sublittorale" by Ouspenskaia (1960). Stark (1965) reports that of the many thousands of specimens of seven species of gammarids examined from the estuary of the Esk River, *Diplocotyle* sp. was only found in the brackish-water species *Gammarus zaddachi zaddachi* between the months of December and April. In Scotland our material was obtained only between February and June and in Newfoundland in May and June. Other records (Table 1) were not dated. Thus, as in the fish host, there is clearly a fairly strict seasonal occurrence in gammarids.

One interesting point that emerges is that, with the exception of the few individuals collected in Scotland in late February and early March which were small and immature, all our material from gammarids was gravid and this is the case for all other reports. Stark's (1965) material was nearly all gravid and he recorded that "no earlier developmental stages were found despite careful scrutiny of large samples of the *Gammarus* population taken in the autumn and winter months." This suggests that the growth and maturation of the larval worm is extremely rapid and perhaps coincides with the short spring burst of activity and growth of the gammarid host.

Stark attributes the complete disappearance of parasitized gammarids after the end of April in the Esk to their selection by predators or to premature death. The behavior of the host is markedly affected by the presence of the parasite, the parasitized individuals becoming sluggish and tending to float upwards from the bottom where they normally hide. Stark also suggests a "dilution" of the parasitized individuals by the decline of the sexually mature fraction of the overwintering population and replacement by the spring brood. Dogiel and Volkova (1946) also observed that the capacity of parasitized amphipods to move is visibly diminished, which increases their chances of being caught and swallowed by a fish. Sudarikov and Kurochkin (1964) attribute the high infestation rate of the gammarids they found among plant debris, thrown up onto the shore after a storm, to the weakness of the parasitized individuals and their inability to hide effectively in wave activity.

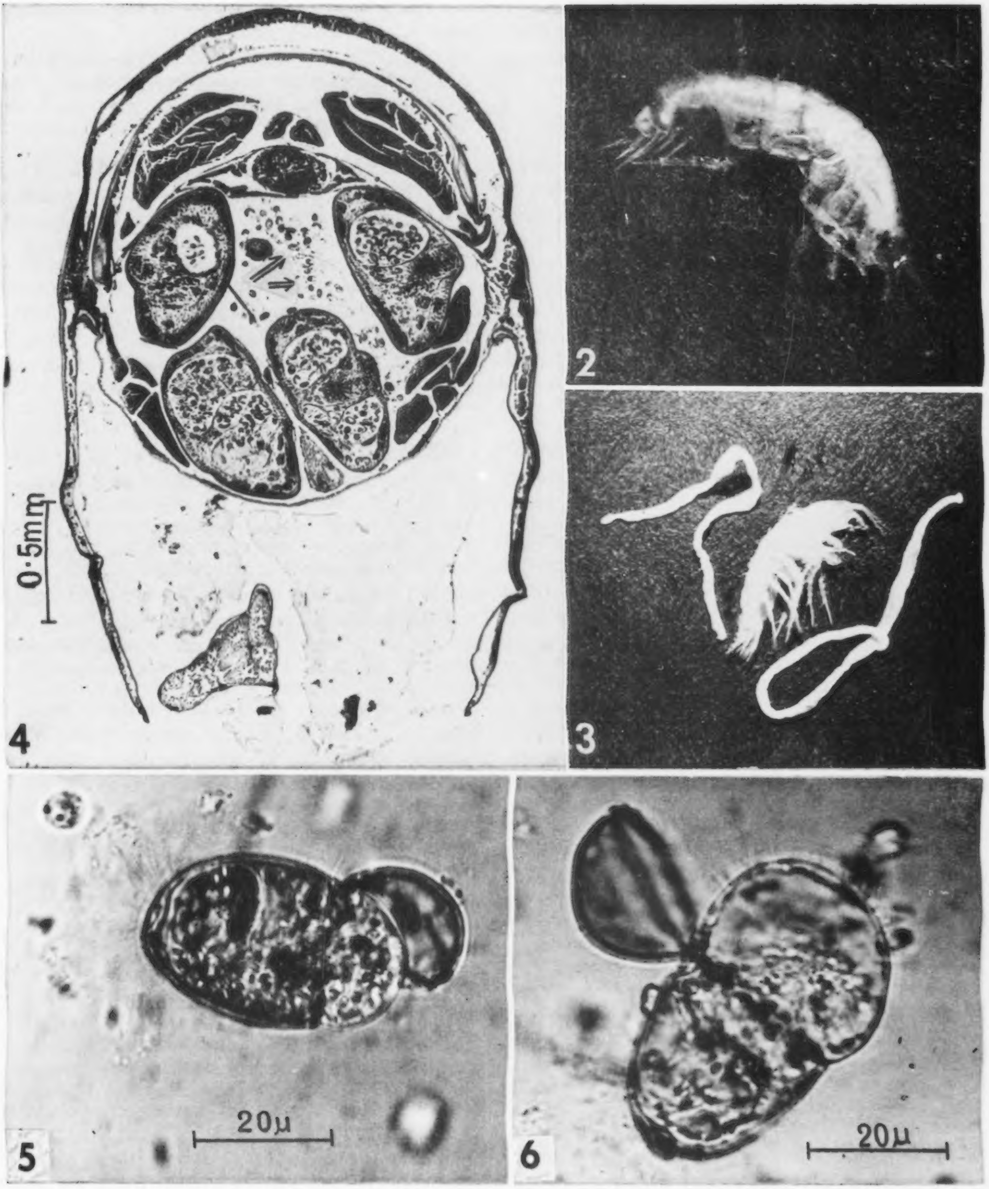
Another quite striking feature of the larval phase of the life cycle is the variety of gammarid species involved, and this apparently conflicts with the strict specificity of the parasite for *G. zaddachi zaddachi* in the Esk indicated by Stark. However, he also points out that there is little overlap of this species with others in the estuary. Thus, the specificity could be ecological in nature and depend upon such factors as the eggs of the parasite requiring certain optimum conditions of salinity or temperature for their maturation, similar to those conditions required by the "preferred" host; the feeding methods and habits of the various gammarids present; or temporal differences in the various stages of development of the gammarids. The fact that a strict specificity was recorded in the Esk would not, therefore, preclude different gammarids being utilized in the range of localities from the Arctic to the Mediterranean and Caspian seas.

Entry into the Vertebrate Host

The closely related genus *Cyathocephalus* has a life cycle involving the freshwater gammarids *Gammarus pulex*, *Rivulogammarus spinicaudatus*, and *Pontogammarus bosniacus* in Europe and *Pontoporeia affinis* in North America, which are ingested by the fish hosts; there is little doubt that *Bothrimonus* also gains entry to the fish host when a parasitized gammarid is eaten.

Attempts to infect *Pleuronectes platessa* and *Salmo trutta* in the laboratory met with only limited success. In one experiment carried out in Scotland, single living plerocercoids were introduced with an eye dropper into the esophagus of each of two plaice and two trout, but no worms were recovered after a week. A second experiment involved the introduction of single worms directly into the stomachs of four plaice and four trout using a thin piece of soft plastic tubing and a syringe. After 24 hr a fish of each species was examined and worms were recovered from both. After 48 hr another fish of each species was examined and a worm was recovered from the plaice but not from the trout. The remaining fish were dissected after a further 48 hr but no worms were found. The specimens that were recovered were active and attached to the intestinal walls of their hosts. In another experiment whole parasitized gammarids were introduced into the diet of ground hard-boiled egg and fish that was regularly being force-fed to a batch of plaice. Gammarids were given to six fish, two of which were examined at intervals of 48 hr, but no worms were recovered. The rather limited scope of these experiments does not permit conclusions to be drawn about the longevity of the parasite in its fish host. The poor success in establishing the worms in a fish host may be due to a very short life-span within the fish but it could also be due to difficulties similar to those experienced by Calentine (1964) in establishing the caryophyllaeid *Archigetes iowensis*, which is also seasonal in its host the carp.

The size and frequency of infection depends upon the availability of parasitized gammarids and the feeding habits and movements of the host. Because of its limited life span and estuarine distribution, *Bothrimonus* may be a useful indicator of the recent feeding behavior of its fish hosts. For example, the presence of *Bothrimonus* in salmon smolts in the lower reaches of the Gander, Terra Nova, and Great Codroy rivers indicates that the smolts move backwards and forwards between the estuaries and lower reaches of those rivers. Unfortunately, no studies have been made which directly link a population of the parasite in gammarids with a population in the fish host in the same locality. However, the biology of the host fish does tie in with what is known of the biology of the parasite: *Pseudopleuronectes americanus* in Passamaquoddy Bay, N.B., not only had a high infestation late in June, but also had fairly heavy parasite loads (up to 50–60 per fish). The movements of this species have been studied by McCracken (1963) who indicates for this area that, during spawning time in May, mature fish of all ages are concentrated in the shallows between 0–5 fath and that, throughout the summer, catches of mature fish of all ages remained greatest there. The concentration is much reduced by November and, in the winter, mature flounders are not taken in shallow water. Immature fish are most common in shallow water from May to July but also move to the deeper water by November. Stomach contents have been studied by A. V. Tyler of the Fisheries Research Board of Canada in the Biological Station at St. Andrews, N.B. (personal communication), who finds that, during



FIGURES 2–6.

FIG. 2. (Gammarid with *Bothrimonus*) A worm visible within the hemocoel of its host; FIG. 3. (Gammarid with *Bothrimonus*) Two worms freshly dissected from their host; FIG. 4. Section of gammarid containing *Bothrimonus*. Arrow indicates eggs of *Bothrimonus*; FIG. 5. Egg of *Bothrimonus* with partly open operculum; FIG. 6. Egg of *Bothrimonus* with fully open operculum.

the feeding period, gammarids form a significant part of the diet, but the winter flounders in Passamaquoddy Bay cease feeding from November to April. These movements and feeding habits of the winter flounder are consistent with the seasonal incidence of the parasite in the invertebrate host.

Salmonids show a considerable variation in the timing of their migrations. In Newfoundland parasitized gammarids have been found in late May and in June. In a survey of freshwater salmonids of Newfoundland carried out from 1963 to 1965 by Sandeman and Pippy (1967), this parasite was not recovered from any salmonids caught inland. Since that survey, *Bothrimonus* has been found in Atlantic salmon smolts in June from the lower section of several rivers. While the information is rather limited, it does tie in with the fact that the early spring and the fall runs of salmon miss the peak infection in gammarids but the June migration of smolts to the sea coincides with it. Stark (1965) suggested that, in the Esk, migrating salmon smolts become infected about April and the reinfection of the gammarid population would occur when the returning spawning migration run took place (early winter). However, as has been pointed out, there is no evidence that the parasite can remain in its fish host for any length of time and this hypothesis is therefore untenable.

Dogiel and Markov (1937) studied the parasites of Arctic char in various phases of its life cycle in Novaya Zemlya. They did not record the parasite from young fish migrating downward to the gulfs and river mouths for the first time after spending 3–4 years in fresh water. However, they found the parasite in both "summer" and "autumn" fish. The "summer" fish are those which descend from the rivers in June and July; they return after a brief sojourn in the sea in August and September as "autumn" fish. During the short marine phase it was apparent from their other parasites that the char forged widely for food: estuarine parasites recorded were *Bothrimonus* and *Metechinorhynchus salmonis*; littoral or marine coast parasites included *Derogenes varicus* and *Podocotyle atomon*; and planktonic parasites were represented by *Lecithaster gibbosus*, *Brachyphallus crenatus*, and *Hemiurus levinseni*. Although the majority of freshwater parasites disappeared by August and planktonic forms predominated, the char continued to feed on littoral gammarids as indicated by the increase from 4 to 28% in the infestation rate of *Echinorhynchus gadi* which has as its intermediate hosts *Pontoporeia femorata* and *Gammarus locusta*. The fact that *Bothrimonus* was still present in the autumn fish although not so common (68% infestation in June–July, 28% in August) would therefore indicate that *Bothrimonus* was still present in gammarids in August, and thus the whole of the char's marine phase coincided with the occurrence of *Bothrimonus* in gammarids in that area.

Entry into the Gammarid Host

The smallest plerocercoids among our material from gammarids and the smallest young individuals from fish lack a cercomer and oncosphere hooks. What happens between the release of eggs on the death of the gammarid host or from the gravid worms within, or discharged from, the fish host and their reappearance in gammarids is not known with certainty.

Attempts were made to observe the maturation and the hatching of eggs: freshly extruded eggs were placed loose in vessels with varying concentrations of sea water and maintained at different temperatures, or were attached to coverslips which were then placed in sea water, and could be removed for examination at intervals. In one series of experiments eggs were allowed to adhere to coverslips which were actually the windows of a small cell. This plexiglass cell had openings through which sea water was passed continuously and the cell was mounted on the stage of a microscope so that eggs could be observed continuously under high power. Within 2–3 days the operculum was seen to open but this was always followed by the swelling and disintegration of the contents (Fig. 5 and 6).

That the eggs opened in the manner described, whether or not the eggs had reached a state of development in which an oncosphere could be recognized, indicates that the opening of the eggs was an abnormal event due to unsuitable physical conditions, either of temperature or salinity. Although large numbers of living eggs were examined, on no occasion was any hint of ciliation of the larva observed.

Attempts were also made over several years to experimentally infect gammarids. Freshly extruded eggs were dropped onto fronds of *Fucus* upon which gammarids were observed feeding. The eggs appeared to be adhering quite strongly to the *Fucus* by means of the fine polar filaments (Fig. 5) and the fronds were placed in aquaria containing gammarids. Whole worms were also placed in aquaria with gammarids and left for several months. The gammarids were removed at intervals and examined both by dissection and sectioning but no developmental stages were recovered.

Of the various alternatives that are open, Stark (1965) considered the possibility that an earlier intermediate host might be involved but dismissed it because "a procercoid typical of other cestodes would be unlikely to survive the masticatory processes of these amphipods in its transference from a first host to *Gammarus*." A second possibility is that a free swimming larva is released from the egg; but this also seems unlikely in view of our failure to observe any ciliation of the larvae. The third possibility, that hatching of an unciliated larva takes place on ingestion of the egg by the gammarid host, seems much more likely as this is the route by which *Cyathocephalus* enters its gammarid host.

Our failure to infect gammarids experimentally could have been due to a number of factors including an unsuitable combination of physical conditions. The state of development of the eggs may also be an important factor. Of the eggs released by our living worms from fish hosts some ten percent have oncosphere hooks; this percentage is smaller for eggs released from worms taken from gammarid hosts and presumably some time is needed to complete the maturation of the eggs before they are infective. Wisniewski reported that there were no hooks in the oncospheres of *Cyathocephalus*, Wardle and McLeod (1952) mention that embryo hooks were figured for that species by Gauthier (1923). This suggests that embryonation may take some time, and it seems likely that the same holds true for *Bothrimonus*. Calentine (1965) reported that eggs of the caryophyllaeid *Biacetabulum* remained infective for 230 days when maintained at 5–10 C and it is not unreasonable to surmise that eggs of *Bothrimonus* could remain attached to natural objects, such as seaweed, by the adhesive hairlike filaments for a considerable time until being eaten by a gammarid. Reports by Wisniewski (1932) and Calentine (1964) indicate that young hosts have a greater susceptibility than older hosts for the closely related worms *Cyathocephalus* and *Archigetes*. It would appear, accordingly, that the most likely sequence for *Bothrimonus* would be that eggs released in summer become attached to seaweed, or other natural objects where the oncospheres complete their development, and remain until they are eaten by a young gammarid. After overwintering these young gammarids mature rapidly and so, probably, do the parasites within them.

The eggs and development of the oncosphere in the gammarid host appear to be identical in every respect with those produced within a fish host. Our failure to infect gammarids experimentally with eggs derived from worms obtained from other gammarids does not preclude the possibility that a fish host may not be necessary for completion of the life cycle. Kennedy (1965) reported a situation for the caryophyllaeid *Archigetes limnodrili* in which the fish host is not necessary and a similar situation is also reported for *A. iowensis* by Calentine (1964). In the latter instance there is a strictly seasonal occurrence in fish but relatively few gravid individuals were found in the annelid host. Kennedy (1965) suggested that *A. iowensis* includes two strains, one of which reproduces exclusively by progenesis and a second which reproduces in the fish host. Wisniewski (1930) indicated that progenesis was the only type of development found under natural and experimental conditions for *A. sieboldi* but more recently, as reported by Kennedy (1965), *A. sieboldi* has been shown to have a strictly seasonal occurrence in fishes. Another possibility for *Bothrimonus*, as suggested by Kennedy for *Archigetes*, is that the incidence and importance of progenetic development may well vary with the locality and species of the intermediate host. Quite a variety of gammarids from different geographical areas and living circumstances are in fact involved and considerable differences in details of the life cycle may be expected. It is also logical to surmise that, as the major part of the development of *Bothrimonus* undoubtedly takes place in the gammarid host, variations in structure in the adult worms should also be related to the conditions in the invertebrate host rather than to the species of fish host, if indeed there is one. It is usually stated for *Cyathocephalus* that eggs are not produced in the amphipod host but we have examined specimens collected from *Gammarus* sp. in March (sent to one of us (I.M.S.) by Mr. B. H. Hall of the University of Leicester) in which eggs are present in the uterus (further investigation may indicate a similar progenetic life cycle for this form in limited localities).

Effect of the Parasite on its Hosts

Stark (1965) noted that, although male and female gammarids were equally susceptible to *Bothrimonus*, the parasite had a different effect on the sexes. Males differed little in size but parasitized females were significantly larger than normal individuals and he suggested that the parasite affects the physiological state of the host gammarid. Stark also suggested that the location of the parasite within the host interferes mechanically with the growth of the gonad in the female and he observed that no trace of ovary could be found in parasitized females and the oostegites of these animals exhibited the bristle-less condition characteristic of the nonbreeding female. In our experience the worms were usually found singly in the hemocoel, however, two were not uncommon and, on one occasion, a gammarid harboring three worms was found. The weight of the parasite may exceed that of the host and, as can be seen in Fig. 4, the worm occupies considerable space in the hemocoel in which it is folded several times. The gonads of the hosts were much smaller than those of unparasitized gammarids and the hepatic diverticulae were smaller and displaced dorsally. The effect of the parasite on the behavior of the host has been mentioned elsewhere.

Large numbers of *Bothrimonus* have, on occasions, been found in the intestines of their fish hosts: Petrushevskii, Mosevich, and Shchupakov (1948); for example, reported 1482 in a single specimen of *Coregonus autumnalis*. Such large infestations have led several authors, e.g. Petrushevskii and Bauer (1948), Dogiel and Markov (1937), and Bauer (1958) to suggest that the species can be pathogenic and that mechanical obstruction, irritation of the intestinal wall, and food deprivation may result from the presence of this parasite. Although quite high parasite loads were present in *Pseudopleuronectes americanus* from New Brunswick, we did not observe any signs of irritation of the host's intestine. In view of the lack of reports of evidence of damage to the host and the relatively short period of time that the parasite spends in the fish host we are doubtful whether *Bothrimonus* should be classified as a pathogen of economic importance.

Distribution and Evolution

Bothrimonus together with the closely related *Cyathocephalus* and Caryophyllaeidae are often referred to as neotenic procercoids or plerocercoids which have lost the ability to migrate out of the gut and into the body cavity of their fish host (this latter host being the second intermediate host in a life cycle in which the definitive host is presumed to have been lost). Development of their reproductive apparatus is completed in the invertebrate host and egg production commonly commences after entry to the fish host is achieved. However, in several species of *Archigetes* the life cycle has been shortened even further; eggs are produced in the invertebrate host and the fish host has been eliminated. Although there is at present no experimental evidence that the eggs produced by *Bothrimonus* while in its gammarid host are viable, it seems likely that a similar situation to that in *Archigetes* may exist for *Bothrimonus*, i.e. that the life cycle may be completed without the fish host. The phase in a fish host, if any, may have a function in dissemination.

While the tendency towards a reduction in the number of hosts in the life cycle and the flexibility shown in regard to the host species may be of considerable adaptive value to *Bothrimonus* it also makes more difficult the interpretation of the present distribution of the species in terms of its recent evolutionary history. The paucity of records of *Bothrimonus* from its gammarid host and the variety of gammarids utilised on the few occasions on which it has been found make it impossible to ascribe *Bothrimonus* to a particular gammarid or group of gammarids, the evolution of which might give a clue to the past history of the parasite. Similarly, with the greater variety of recorded fish hosts the designation of a "normal" fish host is difficult. However, a clue is perhaps given by the closely related *Cyathocephalus* which is a parasite mainly of salmonids. The indication of a second possibility may come from the Caspian form of *Bothrimonus* which has only been found in sturgeons, but in which it reaches a larger size. It is felt, however, that neither of these indications is particularly strong because among the caryophyllaeid worms the dominant fish hosts vary with the geographical region. For instance, Mackiewicz (1959) reports the dominant hosts in the Nearctic region to be catostomids; in the Palearctic region, cyprinids; and in the Oriental, Ethiopian, and Austrian faunal regions, silurid fishes.

Zhukov (1963) discussed in some detail the distribution of the species in the Baltic. He regarded *Bothrimonus* as strictly arctic and marine with its distribution limited on one hand by increases in temperature and on the other hand by decreases in salinity. His view was that *Bothrimonus* is present in the Baltic as a relict of the Yoldian Sea which resulted from cold saline waters rushing into the Baltic Ice Lake Sea (fresh water) some 13,000 years ago. Zhukov argued that the greatest likelihood was that *Bothrimonus* penetrated from the White Sea via lakes Ladoga and Onega. Apart from the fact that this connection has not been definitely established, the Yoldian Sea was replaced by the freshwater Ancylus Lake, and this would not fit Zhukov's hypotheses. Zhukov also argued from the absence of the species from the Atlantic Seaboard of Scandinavia but more recently this gap has been somewhat bridged by the discovery of *Bothrimonus* on the east coast of the British Isles; this makes much more feasible an alternative route of entry to the Baltic Sea via the North Sea.

The occurrence of *Bothrimonus* in the Mediterranean, Black, and Caspian seas raises another interesting problem. The material from the Caspian has been recorded in the gammarid *Dikerogammarus* and from sturgeons and has been ascribed by most recent authors to the species *Bothrimonus fallax* Lühe. This material differs from the more northerly forms in the larger size of the worm, the extent of the vitellaria, and the form of the scolex. We have already indicated (Burt and Sandeman 1969) that differences in the extent of the vitellaria are related to the size of the worm, and a detailed study of the morphology of the scolex (to be presented later) confirms the observations already made concerning the variability of the scolex and the tendency for the single opening characteristic of *B. fallax* to be associated with larger worm size. Our conclusion was that it is doubtful whether the Caspian material should be accorded specific rank on the basis of larger size which may be related to other factors such as temperature of the more favorable conditions for growth in the hosts of that region. The Mediterranean material is poorly described but there are indications that in the characters discussed above, it is intermediate between the Caspian and the more northerly material.

It is possible to account for the present distribution of *Bothrimonus* in the Mediterranean, Black, and Caspian seas in a number of ways: 1. The association of the Caspian form with *Dikerogammarus* and sturgeons suggests that *Bothrimonus* might be, together with the majority of species of the Caspian fauna, an ancient survivor of the fully marine Middle Miocene Basin which had a wide contact with the Mediterranean and formed part of the disappearing Tethys Sea. Polyansky (1958) included *Bothrimonus* in a list of such species. 2. However, the fact that *Bothrimonus* shows little specificity for the gammarid host and that it is a brackish water rather than marine species, would allow for a much later introduction to the Black and Caspian seas from the Mediterranean. These seas have been connected on a number of occasions in the late Miocene (e.g. Maeotic Basin), Pliocene, and Quaternary periods. In the latter the Uzunlar Basin (Mindel–Riss interglacial) and Karangat Sea (Riss–Würm interglacial) were linked with the Mediterranean and access to the Caspian could have been gained via the Kumo–Manych depression (connecting the Novo Euxine lake–sea with the Khavalyn basin during the Würm glaciation). 3. The predominantly circumpolar cold water distribution of *Bothrimonus* suggests a third possibility, namely that it may have been introduced into the Caspian along with other, fairly common, arctic relicts or pseudo-relicts which include both gammarids and salmonids. The Caspian arctic relict fauna may have had its origin in the Baltic or Kara Seas and *Bothrimonus* is present in both these areas, but there is little agreement as to the date at which the introduction took place. Links of the above areas have been suggested at the end of the tertiary, in one or more of the interglacial periods, and in the postglacial era. The link is usually quoted as being freshwater in character and, in view of the evidence that *Bothrimonus* is unable to survive for long periods in fresh water, a recent introduction via fresh water seems unlikely.

These three theories are based on the premise that *Bothrimonus* has a marine and arctic origin but there are arguments to the contrary. First, the closely related *Cyathocephalus* and the caryophyllaeids are freshwater; second, the adoption of a brackish-water environment from a marine habitat over a wide front, without leaving marine relatives, seems improbable; third, unless the adoption of the brackish-water environment was postglacial the arctic would not have provided a suitable habitat during the colder glacial periods of the Pleistocene; and, finally, the distribution and direction of the sea currents would make movement of the species from the arctic southwards to the Mediterranean Sea difficult, but not impossible if the fish host is involved in dissemination.

A number of models could be constructed relating the present distribution of *Bothrimonus* to a freshwater origin. We would suggest the following steps: 1, An ancestral form with a life cycle involving freshwater gammarids and anadromous acipenserid or isospondyl fish hosts, but without strict host specificity and perhaps already with a tendency towards reduction of the phase in the fish host; 2, Adoption of a brackish, cold-water environment; 3, Dispersal of the species to its present circumpolar distribution.

It seems possible from the present distribution of *Bothrimonus* (and *Cyathocephalus*) that these steps took place in one or more of the river systems of the Ponto–Aralo–Caspian Province in the general land mass between the Carpathian and Ural mountain chains. If this is the case then the adoption of the brackish, cold-water habitat probably took place in the Pleistocene as a result of the Scandinavian Ice Sheets, particularly of the penultimate (Riss) glaciation. In this glacial period the ice pressed furthest to the south; fingers extended along the valleys of the rivers to within 200–300 miles of the coast, bringing the remaining land masses to the north of the Caspian and Black seas well within the periglacial area. The hosts of *Bothrimonus* would be pushed southwards by the ice, and the unsuitability of conditions in the remaining stretches of the rivers may well have forced *Bothrimonus* into brackish water. It would also have acquired at this time the tolerance for arctic conditions.

The final step would consist first of westward dispersal through the Caspian and Black seas to the Mediterranean via the links referred to earlier and secondly of a northerly movement, aided by the currents and fish hosts, towards the arctic and its present circumpolar distribution.

Indirect support for this hypothesis comes from the distribution of the closely related *Cyathocephalus* which Shulman (1958) reports as being present over the whole of Europe and northern Asia but absent from the Ponto–Aralo–Caspian Province and the subregion of Upper Asia (with the exception of the Caspian District into which it could have gained entry more recently in post glacial times from the Baltic Province by way of the Volga River). The absence of *Cyathocephalus* from the Ponto–

Aralo–Caspian Province can be explained if the same southerly extension of the Scandinavian Ice Sheets that pushed *Bothrimonus* into its brackish environment eliminated the hosts of Cyathocephalus.

Conclusions

1, *Bothrimonus* occurs in a wide variety of fish hosts of which no single species can be singled out as the "normal" host. The fish hosts have in common the fact that at some stage in their life they feed in littoral or estuarine conditions.

2, The distribution of *Bothrimonus* is circumpolar in boreal or subarctic conditions. Occasionally the species is found living in the high arctic.

3, *Bothrimonus* is short-lived in the fish host and its occurrence in the fish host is seasonal. The length and time of year of the season depend upon the hydrological and climatic conditions in any particular area. The seasonal occurrence in the fish host coincides with the seasonal maturation of *Bothrimonus* in its larval host.

4, There is little doubt that a single intermediate host is involved in the life cycle, and this is a gammarid most commonly from brackish water. Although there may be a fairly strict specificity in any one locality, quite a variety of species of gammarid are parasitized in different geographical areas.

5, The development of larval *Bothrimonus* is neotenic and eggs containing hexacanth larvae are produced while within the hemocoel of the gammarid host. As the major part of the growth and development of *Bothrimonus* takes place within the gammarid host, differences in the morphology of the adult (e.g. the degree of progenesis) should probably be more correctly related to the species and condition of the invertebrate host rather than to the fish host.

6, It is not known with certainty whether the life cycle of *Bothrimonus* can be completed without a stage in a fish host. Embryonated eggs produced within the gammarid host are apparently normal. It is likely that the relative importance of the progenetic development may vary with the locality, the physical environment, and the species and condition of the gammarid host.

7, The suggested life cycle is summarized as follows: Eggs released from gravid worms in the summer adhere to natural objects in the water by means of their polar filaments. The embryos complete their development. On ingestion by a gammarid host an unciliated hexacanth larva emerges from the egg via the opercular opening and enters the hemocoel of the host. Overwintering takes place either within the egg or within a member of the overwintering population of gammarids. In the spring, growth and maturation of the parasite is rapid. Entry to the fish host is by ingestion of the gammarid. Further growth and maturation may take place in the fish host, in which dispersal is effected.

8, There is no evidence for regarding *Bothrimonus* as a pathogen of fish of economic importance.

9, The effect of the parasite on the invertebrate host is pronounced; gonad development is inhibited; there are changes in the pigmentation and secondary sexual characters; modifications to behavior occur.

10, The evolution of the species has two important features: flexibility in the utilization of both its vertebrate and invertebrate hosts, and the tendency towards a reduction in dependency on the fish host.

11, The modern distribution of *Bothrimonus* can be explained on the basis of a temperate freshwater ancestry in the Ponto–Aralo–Caspian region involving freshwater gammarids and possibly anadromous isospondyl or acipenserid fish hosts. Adaptation to the cold, brackish-water environment took place as the species was pushed to the shores of the Caspian and Black seas by the southern extension of the ice during the glacial eras of the Pleistocene. This was followed by a northerly dispersion, via the Mediterranean, using the northerly flowing currents and fish hosts, to the modern circumpolar distribution.

12, The structure of the egg, the unciliated oncosphere, and the nature of the life cycle confirm the close relation (indicated by the morphology of adult worms) between *Bothrimonus* and *Cyathocephalus*. They also suggest closer affinities to caryophyllaeid rather than to other pseudophyllidean cestodes.

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An Application of Louver Deflectors for Guiding Atlantic Salmon (*Salmo salar*) Smolts From Power Turbines

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DUCHARME, L. J. A. 1972. An application of louver deflectors for guiding Atlantic salmon (*Salmo salar*) smolts from power turbines. J. Fish. Res. Bd. Canada 29: 1397–1404.

Louver deflectors for guiding Atlantic salmon (*Salmo salar*) away from destructive power turbines were installed in a canal leading to the powerhouse at East River, Sheet Harbour, Nova Scotia, in 1966. Guiding efficiency studies, using hatchery-reared smolts, showed that a minimum approach:bypass velocity ratio of 1.0:1.5 was a prerequisite to high guiding efficiency. From 1967 to 1971, average guiding efficiency was increased from 57% to 80% through modifications which increased velocity and reduced flow turbulence in the bypass. A significant correlation existed between approach velocity and guiding efficiency within the range tested after bypass hydraulics had been modified. Tests conducted with varying louver bar spacing ranging from 5.1 to 30.5 cm (2–12 inches) showed that the wider spacings did not impair guiding efficiency.

Vertical distribution of smolt migrants in the power canal indicated that over 80% of the fish remained above depth 1.3 m. This was borne out by the fact that the bypass was effective when operating to a depth of only 0.91 m. An appraisal of the practicality of the louver guiding system is presented.

DUCHARME, L. J. A. 1972. An application of louver deflectors for guiding Atlantic salmon (*Salmo salar*) smolts from power turbines. J. Fish. Res. Bd. Canada 29: 1397–1404.

Un essai visant à détourner les jeunes saumons atlantiques de l'entrée d'eau des turbines fut entrepris à la station hydroélectrique de Sheet Harbour, Nouvelle-Ecosse, en 1966. Des grillages du type persienne furent installés dans le canal d'amenée. Une étude d'efficacité, utilisant des smolts de pisciculture, a démontré qu'un rapport de 1.0:1.5 entre la vitesse d'approche et la vitesse terminale du courant (conduit d'évitement) est une condition préalable à l'obtention d'une haute efficacité. Cinq années d'expériences ont permis d'augmenter l'efficacité de l'appareil de 57 à 80% au moyen de modifications visant à augmenter la vitesse du courant et à diminuer la turbulence dans le conduit d'évitement. Il existe une corrélation positive significative entre la vitesse du courant d'approche et le pourcentage d'efficacité de l'appareil. On n'observe aucun changement d'efficacité quand on fait varier l'espacement des lames de 5.1 à 30.5 cm (2 à 12 pouces).

Dans le canal d'amenée, une étude de distribution verticale a indiqué que 80% des smolts se trouvent entre 0 et 1.3 m de profondeur. L'efficacité du conduit d'évitement entre la surface et 0.91 m de profondeur confirme ces résultats. Une évaluation du caractère pratique du système est présentée.

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HYDROELECTRIC development often involves several generating stations in series on the same river system. When a natural run of Atlantic salmon (*Salmo salar*) can be maintained, the greatest difficulty to overcome is the safe passage of juvenile seaward migrants past the power stations.

This problem was experienced in rehabilitation of Atlantic salmon in East River, Nova Scotia, where migrating smolts encountered power intakes at two hydroelectric stations (Fig. 1). Experiments conducted at East River's Malay Falls station with Atlantic salmon smolts revealed an average turbine mortality of 13% (L. J. A. Ducharme unpublished data), which is within the range (10–25%) shown by Cramer and Oligher (1964) for chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Salmo gairdneri*).

Of the most recently developed techniques for the guidance of downstream migrants, louver deflectors as described by Ruggles and Ryan (1964) were selected for their high guiding efficiency, their velocity tolerance, and their sturdiness. Fixed

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screens were ruled out because of high water velocities in the Ruth Falls power canal. Horizontal travelling screens were still at the development stage in 1967 (D. W. Bates personal communication).

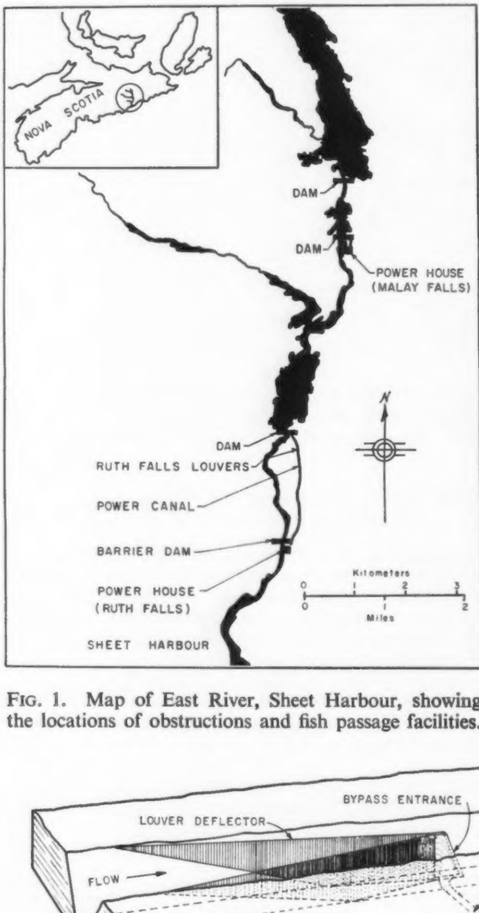
NOVA SCOTIA
DAM
DAM
POWER HOUSE (MALAY FALLS)
N
DAM
RUTH FALLS LOUVERS
POWER CANAL
BARRIER DAM
POWER HOUSE (RUTH FALLS)
SHEET HARBOUR
Kilometers
0 1 2 3
0 1 2
Miles

FIG. 1. Map of East River, Sheet Harbour, showing the locations of obstructions and fish passage facilities.

The usefulness of louver deflectors in diverting juvenile migrants of various salmonid species from a canal or flume was demonstrated by Bates and Vinsonhaler (1957), Bates and Jewett (1961), and Ruggles and Ryan (1964).

A fish guiding facility consisting of two louver lines converging to a single bypass was built in the Ruth Falls diversion canal at East River in 1966. Since louvers had never been used to guide Atlantic salmon juveniles, the facility was experimental as well as a practical means of diverting smolts from turbine intakes. The adaptation and testing of the facility took place from 1967 to 1971.

Materials and Methods

STUDY AREA AND FACILITIES

The Ruth Falls power plant is owned by the Nova Scotia Power Commission. Its operation depends on the state of river discharge as well as on demand for electric power, with the result that frequent load adjustments are made to match that demand. The plant is equipped with three Francis-type turbines, operating on a normal head of 32.5 m. A sidehill canal, 2.13 km long, was necessary to achieve this head. Daily power output varies from 800 to 6900 Kilo Volt Amps (KVA), with corresponding flow variations in the canal from 4.25 to 34 m^3/sec. Water velocity at the upstream end of the canal ranges from 0.30 to 1.09 m/sec.

Except for brief periods in April, the entire river flow is diverted to the power plant, and therefore the canal is the only route available for smolts during their normal downstream migration in the latter part of May. The water from the louver bypass was used to carry smolts diverted from the canal approximately 3.2 km to saltwater via the original river bed.

The louver system (Fig. 2) consisted of two vertical louver lines placed in a V-arrangement at a 12° angle

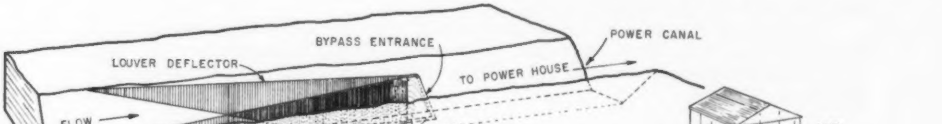
BYPASS ENTRANCE
POWER CANAL
LOUVER DEFLECTOR
TO POWER HOUSE
FLOW
BYPASS PIPELINE
HUT
VALVES
RAMP
TROUGH
VALVE
BYPASS DISCHARGE
FLUME TO OLD RIVERBED
COLLECTION BOX
101'
99'
97'

FIG. 2. Three-dimensional diagram of the Ruth Falls louver deflectors and related facilities.

from the canal wall. The removable louver panels were supported by tubular steel frames 15.2 cm in diameter, permanently anchored to the concrete lining of the canal. The trapezoidal cross section of the canal was 3.96 m high, 12.8 m wide at the normal water surface, and 4.27 m wide at the base. Total length of the louver array was 27.4 m and maximum height of the panels was 4.27 m. The louver slats were placed 5.1 cm (2 inches) apart at a 90° angle to the direction of flow. Every sixth slat was extended to form a flow-straightening vane and was permanently affixed to the panel frame (Fig. 3). By removing one or more slats, louver bar spacing of 10.2, 15.2, and 30.5 cm (4, 6, and 12 inches) were possible. The louver bypass was a design adaptation from a similar installation at Robertson Creek in British Columbia. The width of the bypass was 45 cm and its submerged depth was 3.6 m. Operating under a hydraulic head of 1–1.5 m, the bypass discharged its flow of approximately 1.4 m³/sec via an underground conduit (24.3 m long, 0.91 m in diameter) into a concrete pool parallelling the power canal (Fig. 2). A modified Wolf trap in the pool led fish to an adjacent building containing fish sorting facilities. The excess water was returned to the former river bed.

EXPERIMENTS

The experiments were carried out each May and June from 1967 through 1971. Two-year old hatchery-reared Atlantic salmon smolts, 15.2–17.7 cm in length, were used for most tests. Testing was carried out at night to correspond with the normal nocturnal seaward migration of smolts. Approximately 100 fish per test were used, each group being identified by fin clipping. This was performed on anaesthetized fish 12–24 hr before their release in the power canal. Shortly before the release of test fish, the approach and bypass velocities were measured at 15.2-cm (6-inch) intervals from the surface to a depth of 1.83 m, using an Ott universal water velocity meter. Water temperature, length of fish, power load, head loss, and weather conditions were also recorded. Fish were then released 30 m upstream of the louver entrance.

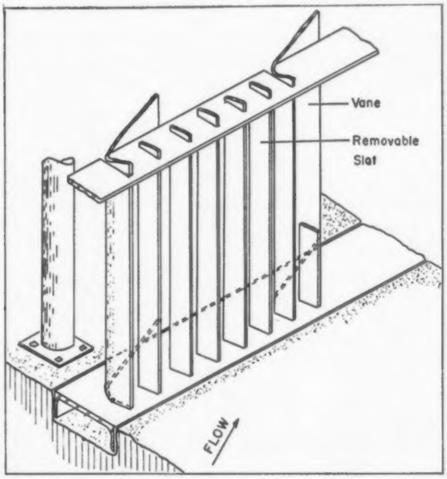

FIG. 3. Detail of louver panel. The vanes are welded on the frames and are overlapping. The removable slats permit spacings of 5.1, 10.2, 15.2, and 30.5 cm (2, 4, 6, and 12 inches).

The recorded fish guiding efficiencies were minimal and were determined by counting the number of test fish caught in the sorting facilities. No corrections were possible for test fish escaping through the louvers, for predation, or for fish remaining in the impoundment above the louver facilities.

Vertical distribution of smolts in the bypass entrance was investigated in May and June 1971. For this purpose the bypass was arbitrarily divided into four 45 cm depth zones from the surface to the bottom of the bypass. A cone-shaped net, 2 m long, 1.2 cm (½ inch) stretched mesh, attached to a steel frame 45 cm square was fixed at various levels in the bypass during normal louver efficiency tests.

Results and Discussion

During 5 years of investigation, 111 tests were conducted with hatchery-reared fish and three tests with wild East River fish. Overall guiding efficiency of the louvers was increased from 57% in 1967 to over 80% in 1970 and 1971, mainly through modifications aimed at increasing water velocity in the bypass. Of all the factors considered, three had a significant influence on the guiding efficiency: (1) the vertical distribution of smolts in the louver bypass; (2) the ratio of approach velocity to bypass velocity,[1] (3) the approach velocity in the power canal.

VERTICAL DISTRIBUTION OF SMOLTS IN LOUVER BYPASS

The results averaged from two series of four tests are presented graphically in Fig. 4. Nearly 80% of the fish recaptured had entered the bypass between 0 and 1.3 m deep. The distribution pattern revealed was essentially a corroboration of the indications obtained in 1968[2], that smolts migrating in the power canal remain well above the 2 m depth level.

Velocity immediately in front of the bypass was not affected by the net. Fish died within minutes of their recapture, as high velocities prevented escape from the net. As only 11.5% of the fish released were recaptured in the net and the overall guiding efficiency for the individual test was otherwise unaffected by the presence of the net, it appeared that smolts were able to sense and evade the apparatus placed in the bypass.

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[1] Subsequently referred to as: "bypass acceleration" and expressed as a percent of approach velocity.

[2] High guiding efficiency was obtained in tests where the bypass intake area extended to only 1 m bleow the surface.

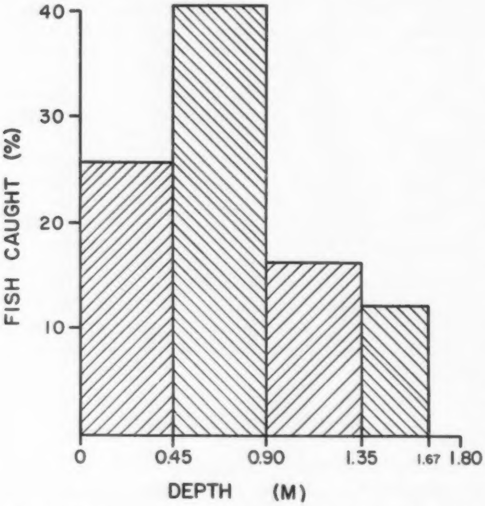

FIG. 4. Diagram of vertical distribution of smolts entering the Ruth Falls louver bypass.

EFFECT OF BYPASS ACCELERATION ON GUIDING EFFICIENCY

Early in 1967, it was observed that: (1) no flow acceleration occurred in the bypass because of its large intake area relative to its hydraulic head; (2) poor vane design led to uneven velocity distribution in the bypass (Fig. 5). In addition, wood debris tended to lodge between the three upper vanes but this problem was solved by installing a trash rack system across the power canal entrance (Fig. 6).

Velocities in the bypass were controlled in 1968 by reducing the bypass aperture in depth by means of wooden panels of various heights (Fig. 7). The lower half of the bypass was permanently blocked in 1969 and its internal structure was modified to produce uniform velocity distribution along its vertical plane and also to reduce turbulence. Finally, in 1970 the bypass hydraulic head was increased from 1 to 1.5 m by lowering the Wolf-trap screen in the bypass discharge pool (Fig. 2).

The 1968 tests were conducted over a wide range of bypass velocity ratios. Data relating guiding effi-

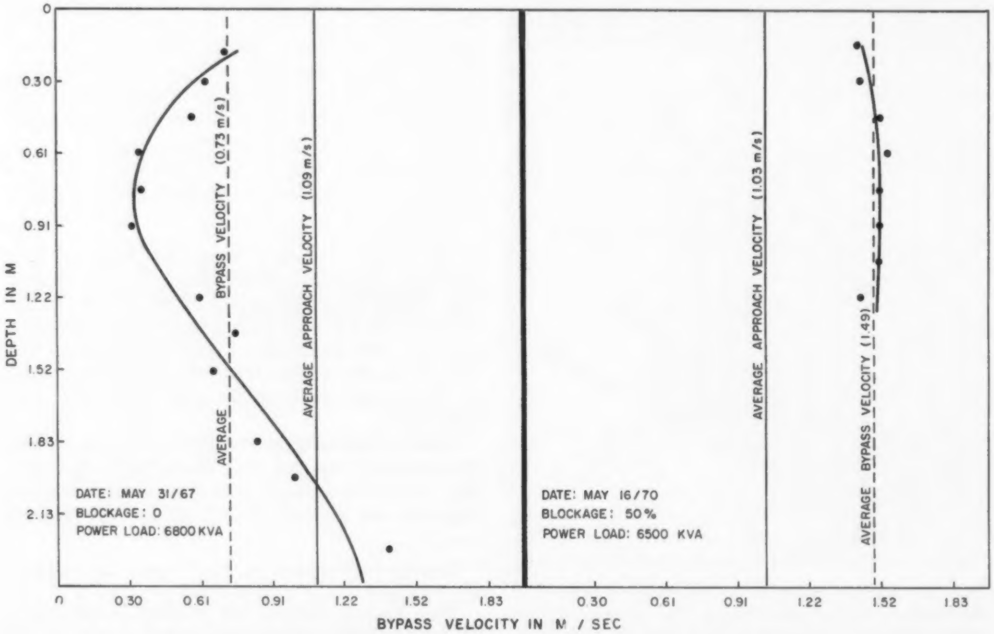

FIG. 5. Vertical velocity distribution at entrance of fish bypass, Ruth Falls louvers 1967–70.

ciency and approach bypass velocity ratio showed that a ratio in the order of 1.0:2.5 was necessary to ensure a level of 80% or more in guiding efficiency (Fig. 8). There were, however, indications that most fish entered the bypass above the depth of 76 cm although the full available opening was then 1.83 m. Average bypass velocity for the various tests was then recalculated for a depth of 76 cm, and the optimum ratio shifted to 1.0:1.5 (Fig. 8). Ruggles and Ryan (1964) and Bates and Vinsonhaler (1957) found that a bypass velocity ratio in the order of 1.0:1.4 was a prerequisite to high guiding efficiency for sockeye, coho, and hcinook juveniles. The results presented in Fig. 8 also show that bypass velocity ratios two or more times greater than the optimum value of 1.0:1.5 did not reduce guiding efficiency. Thus, when circumstances preclude control of approach velocity, which varied over a substantial range at Ruth Falls, the bypass system must be designed to ensure the minimum acceptable bypass acceleration at the highest limit of the approach velocity range. Low approach velocity would necessitate self-regulating controls on bypass flow if constant bypass acceleration is to be maintained to avoid wasting water.

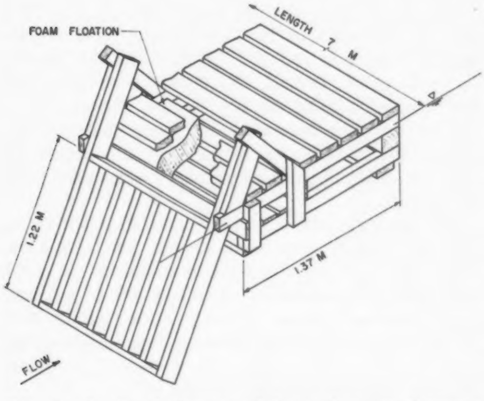

FIG. 6. Sectional diagram of the trash removal system strung across the power canal at Ruth Falls 1969–71. The apparatus was in three 7-m sections.

EFFECT OF APPROACH VELOCITY ON LOUVER GUIDING EFFICIENCY

Water velocity in the canal was not controlled for experimental purposes, and it varied according to the Ruth Falls power station output. Velocities generally remained high during the month of May and were reduced at night in June. The full range of approach velocities experienced was from 0.24 to 1.06 m/sec.

Combined 1968 and 1969 data relating approach velocity and guiding efficiency (Fig. 9A) revealed a negative relationship between guiding efficiency and approach velocity which was statistically significant ($P < 0.001$). Since the bypass shapes, dimensions, and hydraulic head were fixed by design, the velocity in the bypass was not easily adjusted to maintain a constant ratio of approach/bypass velocity. The unfavorable flow conditions in the bypass in 1968 and 1969 masked the otherwise favorable effect of an increase in approach velocity and a negative correlation between approach velocity and guiding efficiency resulted. The 1970 and 1971 tests were conducted with an improved bypass, and there was a weak positive correlation between approach

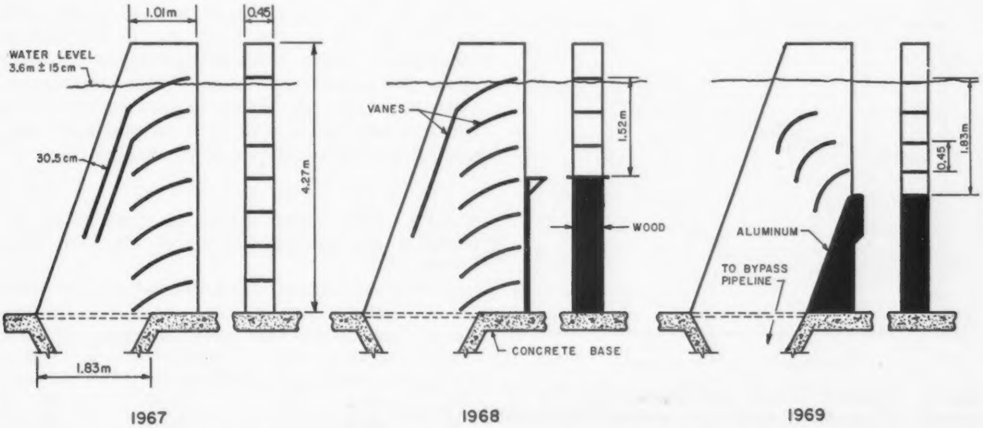

FIG. 7. Diagram of the Ruth Falls louvers bypass evolution 1967–70.

velocity and guiding efficiency which was statistically significant ($P < 0.02$) (Fig. 9B). For analysis purposes, the percentage efficiency results were made to meet the assumption of the analysis by use of the angular transformation table given by Rohlf and Sokal (1969).

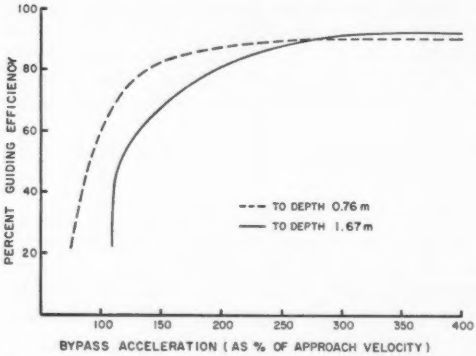

FIG. 8. Bypass acceleration and louver guiding efficiency, Ruth Falls louvers, 1968. Note that optimum acceleration value is much lower when the acceleration was computed from velocities in the fish occupied strata only (0.0–0.76 m).

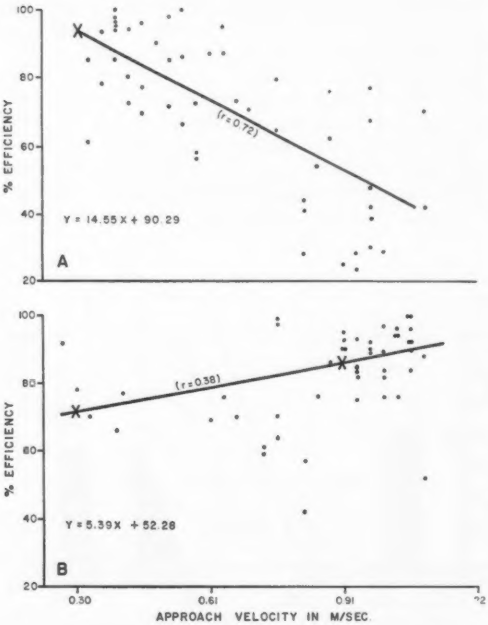

FIG. 9. Approach velocity and guiding efficiency of Atlantic salmon smolts, Ruth Falls (A) using the bypass as originally designed, 1968 and 1969 (B) using a modified bypass 1970 and 1971.

Bates and Jewett (1961) and Ruggles and Ryan (1964) found no significant correlation between approach velocity and louver guiding efficiency, Bates and Vinsonhaler (1957) indicated that within the range tested (0.15–1.8 m/sec) the higher velocities were desirable. This was borne out by the 1970 and 1971 results at Ruth Falls. The higher approach velocities probably compel fish to actively maintain their position relative to the louvers, thus preventing them from wandering.

EFFECT OF BAR SPACING ON GUIDING EFFICIENCY

Louver guiding efficiency was lowered by 18% when bar spacing was increased from 5.1 to 10.2 cm in 1967 (Table 1). Concurrently, the bypass acceleration was reduced by 12% as the greater flow of water through the louver slats decreased the hydraulic head on the bypass (Anon. 1967). After corrective measures had been taken to increase the bypass acceleration to an acceptable level of 1.0:1.27, guiding efficiency was raised from 37 to 73%.

Bar spacings of 10.2, 15.2, and 30.5 cm (4, 6, and 12 inches) were tested from 1968 to 1971. High guiding efficiencies were obtained in 1968 and 1970 with wide bar spacings (30.5 cm) and high approach bypass velocity ratios, but in 1971 it was also possible to maintain high guiding efficiencies with lower ratios by a reduction in bar spacing near the bypass (Table 2).

At low velocities ($V < .50$ m/sec) head losses through louvers were negligible. At high velocities head losses of 6.0 and 13.0 cm were measured for bar spacings of 30.5 and 10.2 cm, respectively (Fig. 10). These head losses were amplified with the distance along the canal due to the relative increase in friction. Since the energy lost by water in an open channel is a function of the initial energy (Vennard 1966), the siting of louvers in a long canal as well as bar spacing is an important consideration relative to power production.

TABLE 1. Effect of bar spacing on mean bypass acceleration and guiding efficiency of the Ruth Falls louvers, 1967.

No. of tests	Bar spacing (*cm*)	Bypass blockage (%)	Approach bypass velocity ratio	Guiding efficiency (%)
4	5.1	–	0.80	55
3	10.2	–	0.68	37
6	10.2	25–65	1.27	73.2

On the basis of the data presented in Table 2, it would appear that louver bar spacings greater than 30.5 cm may be possible with Atlantic salmon smolts. The 1971 results suggest that the most effective arrangement might be a wide bar spacing at the widest part of the louvers, with gradual reduction in bar spacing leading towards the bypass. (Distance 0–9 m, 30.5 cm bar spacing; 9–18 m, 15.2 cm; 18–22.5 m, 10.2 cm and 22.5–27.4 m, 5.1 cm). This arrangement would also result in an economy of bypass water as less acceleration is required.

Studies of the hydraulic characteristics of louvers in Berkshire, England, showed that a greater proportion of flow passes through the downstream end of the louver screens (Anon. 1967); it ensues that the probability of fish passing through the louver screens is increased with distance along it.

There is total agreement in the literature that the maximum acceptable louver slat spacing is related to fish size. Ruggles and Ryan (1964) obtained high guiding efficiencies with sockeye and coho salmon juveniles at 10.2 and 15.2 cm (4 and 6 inches) bar spacing when bypass width and ac-

TABLE 2. Comparative salmon smolt guiding efficiency of the Ruth Falls louvers at bar spacings of 10.2, 15.2, and 30.5 cm (4, 6, and 12 inches). Values are means ± standard error.

Spacing (*cm*)	Year	No. of tests	Approach bypass velocity ratio	Guiding efficiency
10.2	1968	11	2.36±.229	80.3±3.955
10.2	1969	15	1.62±.099	69.9±4.570
15.2	1968	9	3.08±.005	89.8±3.223
15.2	1970	18	1.59±.037	82.3±2.632
30.5	1968	3	3.01±.242	82.7±2.909
30.5	1970	6	1.78±.071	87.3±3.380
30.5>15.2 >10.2>5.0	1971	18	1.34±.033	84.9±3.511

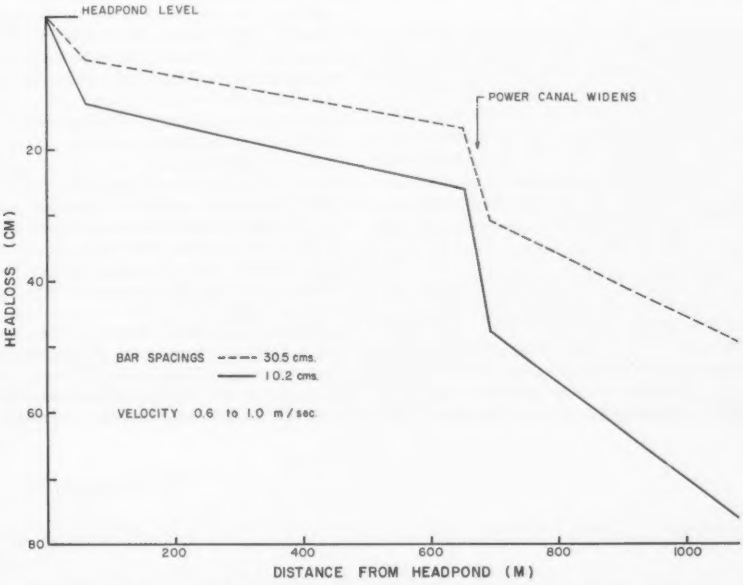

FIG. 10. Diagram of hydraulic head loss through louvers, Ruth Falls 1968.

celeration were ideal. Monan et al. (1967) obtained high louver guiding efficiency with juvenile steelhead trout at bar spacings up to 25.4 cm (10 inches) although the bypass width (15.2 cm) used in these tests is not considered adequate to have ensured a high degree of acceptance by fish as large as steelhead smolts.

Comparative Guiding Efficiency with Wild and Hatchery-Reared Smolts

In the spring of 1969, 18 louver tests made with hatchery smolts gave 66.8% efficiency and three tests with native East River smolts gave 59.3% efficiency. A 2 × 2 contingency analysis showed no significant difference between the two groups ($P > .02$). In addition to tests with hatchery fish, the louvers were tested with two small runs of native smolts in 1970 and 1971. The results suggest that guiding efficiencies between hatchery-reared and wild fish are quite comparable:

	Smolts			
	Hatchery		Wild	
Year	1970	1971	1970	1971
No. released				
Actual	2020	845	682	3273
Fork length (*cm*)	19.3	18.9	17.8	17.7
Corrected			594	2848
Recovered (%)	86	83.7	86	80

Percent guiding efficiencies of the Ruth Falls louvers for the native runs of fish were determined by dividing the number of smolts successfully deflected by the number counted through a fence situated seven miles upstream of the louvers. A correction factor of 13% (L. J. A. Ducharme unpublished data) was introduced for turbine mortality through Malay Falls hydro-station situated on the migration path between the counting fence and the louvers. Natural losses and losses by predation, however, are not accounted for.

These results indicate that, in future application, the louver panels and bypass systems need not exceed a depth of 2 m. Approach velocity and bypass acceleration are related, and both affect louver guiding efficiency. Determination of the minimum bypass acceleration acceptable must take approach velocity into consideration. The possibility of using multiple regression analysis in predicting louver guiding efficiency with various approach velocity and bypass acceleration values was explored but the data available did not lend itself to this exercise. More research is required to determine the maximum permissible bar spacing for Atlantic salmon smolt louver guidance.

It is concluded that louvers are a practical means of guiding Atlantic salmon smolts when the fish must be actively extracted from a narrow, fast-flowing body of water with velocities of 0.61 m/sec or more.

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The author is grateful to Messrs D. B. Lister, C. P. Ruggles, and T. G. Carey (Canada Department of the Environment, Fisheries Service, Resource Development Branch, Halifax, N.S.) for their critical review of the manuscript; and Messrs J. Cameron (Canada Department of the Environment, Fisheries Service, Resource Development Branch, Halifax, N. S.) and J. Keough (University of New Brunswick, Fredericton, N.B.), who conducted the field operations.

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Effects of Controlled Flow Reduction on a Trout Stream

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The total number of brook trout age I and older in three runs of Blacktail Creek, Mont., was reduced approximately 62% when 90% of the normal flow was diverted for about 3 months, in comparison with 20% for runs in control sections. Both number and weight of trout in pools of the test sections generally increased, whereas those in control pools decreased. Recaptures of tagged trout also indicated movements from runs to pools in the test sections, but not in the control sections. When the flow was reduced 75% or less, there were no consistent changes in number or weight of trout in the test runs and pools, whereas those in the control sections were more marked though also inconsistent. Reduced flows had no consistent effect on the number of underyearlings. The changes in most physical characteristics after 90% flow reduction were considerably less than the degree of reduction, presumably because the stream flowed in a well defined channel. Surface area and average depth were least affected (about 42% decrease) and current velocity (75%) the most. Fast-water portions (current velocity over 0.30 m/sec) comprised over 60% of the surface area at normal flows and slow water portions over 85% of the area when the flow was reduced 90%. A multiple linear regression with the physical characteristics as independent variables and the number of trout as the dependent variable accounted for over 75% of the variation in the number of age I and older trout in runs and pools.

Kraft, M. E. 1972. Effects of controlled flow reduction on a trout stream. J. Fish. Res. Bd. Canada 29: 1405–1411.

Le nombre total d'ombles de fontaine d'âge I et plus dans trois secteurs à eau courante du ruisseau Blacktail, Montana, a diminué d'environ 62% lorsque 90% du débit normal du cours d'eau a été détourné durant environ trois mois, comparativement à 20% dans les secteurs témoins. Le nombre et le poids des ombles ont en général augmenté dans les pools des secteurs expérimentaux, alors que ceux des pools témoins ont diminué. Les retours d'ombles marqués indiquent que les poissons se déplacent des rapides vers les pools dans les secteurs expérimentaux, mais non dans les secteurs témoins. Après réduction du débit de 75% ou moins, il n'y a pas de changement uniforme dans le nombre et le poids des ombles des rapides et des pools expérimentaux, alors que dans les secteurs témoins, les changements sont plus marqués, quoique également irréguliers. La réduction du débit n'a eu aucun effet constant sur le nombre d'ombles de moin d'un an. Après réduction du débit de 90%, la plupart des caractéristiques physiques ne changent pas en proportion, sans doute parce que le ruisseau coule sur un lit bien délimité. La superficie et la profondeur moyenne sont le moins affectées (autour de 42% de diminution), et la vitesse du courant l'est le plus (75%). A un débit normal, les secteurs à courant rapide (plus de 0.30 m/sec) constituent plus de 60% de la superficie. Après réduction du débit de 90%, les eaux lentes couvrent plus de 85% de cette superficie. Une régression linéaire multiple, ayant comme variables indépendantes les caractéristiques physiques, et comme variable dépendante le nombre de poissons, rend compte de plus de 75% de la variation du nombre d'ombles d'âge I et plus dans les secteurs à eau courante et dans les pools.

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THIS study was an attempt to determine how various amounts of flow reduction alter the physical characteristics and affect the resident trout population in two types of habitat (runs and pools) in a stream. The Montana Fish and Game Department began a project in 1964 to determine how reduced stream flows affect a trout population (Wipperman 1966). Though Weber (MS 1959) and Curtis (1959) showed the effects of reduced flows on the physical characteristics of rivers, Schiemenz (1960) those on fish movement at changing flows, and Spindler (1955) and Clothier (1953, 1954) those on fish loss in irrigation diversions, little has been reported about how flow reductions affect the habitat and resident fish population in a stream.

Study Area and Methods

The study was conducted on Blacktail Creek from June, 1965 to October, 1967. The creek lies in southwestern Montana and flows through a broad valley with grass covered collescent alluvial fans bordering both sides of the 2.3 km wide flood plain. The stream gradient was 7.6 m/km.

The creek flows in a well defined channel and bank erosion and flooding were uncommon even with a wide range of flows. Flow records (Fig. 1) were obtained from a United States Geological Survey station about 13 km below the study area. The station was discontinued in September 1966, but a flow recorder at the study area showed 1967 flows to be near average.

Chemical analyses made in the study area during August, 1965 showed total alkalinity as 202 ppm and total hardness as 237 ppm. Specific conductance was 284 micromhos. The maximum water temperature recorded during the summer was 20 C.

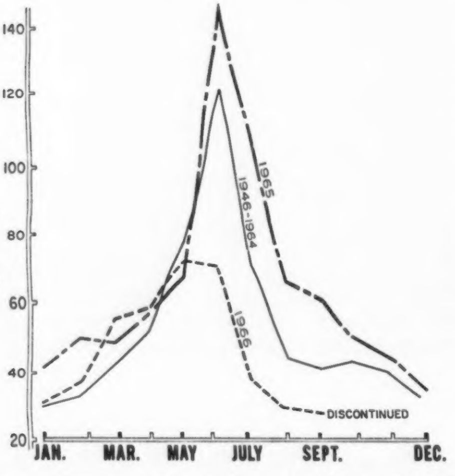

FIG. 1. Mean monthly discharges in 1965 and 1966 and for 1946–1964 at the U.S. Geological Gage Station on Blacktail Creek.

A 520-m portion of the creek was divided into three sections, and a diversion canal was dug so that the flow to each section could be regulated (Fig. 2). Steel headgates for regulating the flow to each section and traps to monitor fish movements out of the study area were installed. Two sections 400 and 800 m from the test sections served as controls. A pool and a run in each of the five sections were selected for intensive study. A pool was defined as a portion of the stream with greater than average depth and less than average velocity and cover. A run was a portion of the stream with about average depth, velocity, and cover. The stream was closed to fishing for 1.5 km above and below the study sections.

The base for flow reduction was determined by considering August flows for the 6 years preceding 1965 and the lowest 3 years were averaged to give about 35 ft^3/sec. In 1965 and 1966, the flow was reduced to 8 ft^3/sec in section A, to 16 ft^3/sec in B, and to 24 ft^3/sec in C. In 1967 all three test sections were reduced about 90%, to 3 ft^3/sec. The flow reduction period was selected to simulate the irrigation season for agricultural crops, which was about 3 months.

Fish populations in all sections were sampled in the spring before flow reduction commenced and in the autumn before normal flows were restored. Sampling was carried out by electrofishing using a 300-v, 850-w direct current unit. Sections and each run or pool within the section were isolated with blocking nets. Three passes per sampling period were made through each area and about 90% of the trout age I and older were collected. Brook trout (*Salvelinus fontinalis*) comprised almost 90% of the fish collected and is the only species dealt with. Underyearling trout were considered separately from older trout, since the younger fish were too small to be collected during the spring sampling periods. Fish were anesthetized with M.S. 222 (Tricane Methanesulfonate), then measured (total length) and weighed.

Trout over 17.5 cm long in the study pools and runs of the test sections and of the lower control were marked with colored plastic jaw tags before flow reduction in 1965 and 1966 to determine movements. In 1967 they were cold-branded as suggested by Everst and Edmundson 1967.

All pools and runs were mapped (width, depth, current velocity, and cover) each summer during reduced flows and at least once when the flow was near 35 ft^3/sec. Transects were established at 1.5-m intervals along the middle of the stream and depth and current velocity were measured every 0.5 m along them. Current velocity was measured with a Gurley current meter at 0.6 of the depth at each location. The water comprising each run or pool

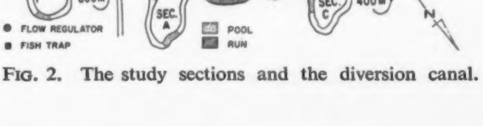

FIG. 2. The study sections and the diversion canal.

was classified according to depth and velocity as follows: Deep-fast > 0.5 m deep and > 0.30 m/sec; Fast-shallow < 0.5 m deep and > 0.30 m/sec; Slow-shallow < 0.5 m deep and < 0.30 m/sec; Deep-slow > 0.5 m deep and < 0.30 m/sec. Cover included overhanging vegetation (dead or alive) and undercut banks. Overhanging vegetation was defined as submerged or within 0.3 m of the water's surface. The amount of cover and each water classification was determined from completed maps with a planimeter.

Population data for the autumn of 1965 were not suitable for determining the effects of flow reductions since sampling occurred during the spawning period and the flow control structure at the beginning of section A was a barrier to migrating fish.

The data were analyzed in a multiple linear regression by the computing centre at Montana State University to determine the relation between physical characteristics of and the number of fish in pools and runs.

Physical Characteristics of Runs and Pools, 1965-67

Surface area, average depth and cover showed a greater reduction in runs than in pools (Table 1). Reduction in current velocity was greater in pools than in runs. Maximum velocity usually decreased less than average velocity. When the flow was reduced 90% the average depth and area of the pools and runs decreased less than 42%, cover decreased 39–56% and average current velocity decreased 71–85%.

Flow reduction resulted in pronounced changes in the water classifications of pools and runs. When the flow was reduced 90% deep-fast portions, which comprised 20% or more of the surface area at normal flow, were eliminated in runs and severely reduced in the pools (Fig. 3). Shallow-fast portions were mark-

TABLE 1. Physical characteristics of the runs and pools in the various sections before and after flow reduction, 1965–1967. Values when flow was reduced to 8, 16, and 24 ft^3/sec are averages for summers of 1965 and 1966; those when flow was reduced to 3 ft^3/sec, for 1967; all others are averages for the 3 years.

Area	Flow	Surface Area (*m*^{2})	Average Depth (*m*)	Velocity (*m/sec*)		Cover (*m*^{2})
				(*avg*)	(*max*)	
Controls						
Upper, run	29	131.2	0.27	0.58	0.82	12.9
pool	29	70.0	0.33	0.47	0.67	18.7
Lower, run	33	231.8	0.39	0.42	0.59	39.6
pool	33	100.5	0.36	0.49	0.72	40.5
Section A						
Run	35	139.1	0.30	0.64	1.00	37.5
	8	105.4	0.21	0.31	0.42	25.9
	3	97.6	0.18	0.17	0.29	17.5
Pool	35	108.1	0.36	0.44	0.63	24.3
	8	86.4	0.30	0.19	0.29	10.6
	3	81.6	0.24	0.10	0.18	11.1
Section B						
Run	35	217.1	0.27	0.54	0.89	38.0
	16	181.8	0.24	0.39	0.61	31.2
	3	138.2	0.18	0.16	0.26	16.4
Pool	35	172.9	0.33	0.46	0.68	37.5
	16	151.3	0.32	0.27	0.50	23.8
	3	143.7	0.27	0.09	0.21	21.5
Section C						
Run	35	162.0	0.36	0.58	0.84	42.8
	24	145.4	0.35	0.47	0.76	29.9
	3	113.8	0.21	0.14	0.27	26.2
Pool	35	141.6	0.36	0.47	0.68	27.5
	24	132.9	0.35	0.34	0.50	23.1
	3	107.2	0.27	0.07	0.14	15.0

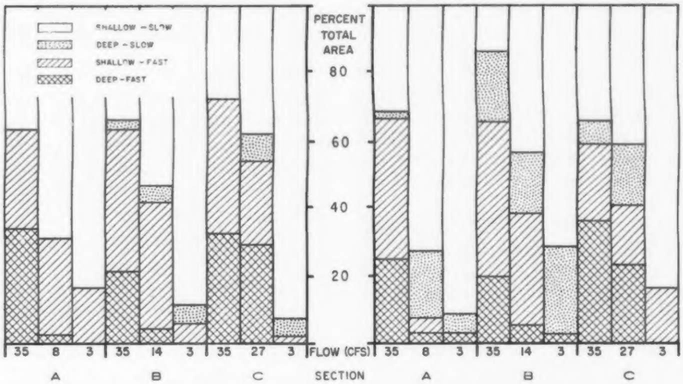

FIG. 3. Percentages of total areas of runs (*left*) and pools (*right*) in the test sections assigned to various water-types at various flows.

TABLE 2. Total numbers and (in parentheses) weights (*kg*) of brook trout age I and older before and after flow reduction in various runs and pools and percent changes, 1966 and 1967.

	1966			1967		
	May	Aug.	(%)	May	Sept.	(%)
			Controls			
Upper, Run	46 (1.75)	23 (1.07)	–50 (–39)	24 (1.72)	11 (0.94)	–54 (–45)
Pool	14 (0.67)	18 (2.34)	+29 (+248)	8 (0.71)	6 (0.44)	–25 (–38)
Lower, Run	78 (4.71)	66 (4.25)	–15 (–10)	52 (3.47)	48 (4.42)	–8 (+27)
Pool	39 (2.22)	30 (2.80)	–23 (+26)	36 (2.35)	24 (2.01)	–33 (–14)
			Section A			
Run	60 (3.34)	48 (2.09)	–20 (–37)	35 (2.30)	28 (1.89)	–20 (–18)
Pool	46 (2.77)	48 (3.85)	+4 (+39)	38 (3.23)	43 (3.64)	+13 (+13)
			Section B			
Run	72 (3.55)	68 (3.29)	–6 (–7)	54 (2.29)	13 (0.60)	–76 (–74)
Pool	57 (4.56)	55 (5.60)	–4 (+23)	63 (4.51)	58 (5.27)	–8 (+17)
			Section C			
Run	64 (3.73)	73 (5.54)	+14 (+49)	79 (5.76)	23 (2.36)	–71 (–59)
Pool	60 (4.34)	59 (3.79)	–2 (–13)	32 (2.28)	40 (3.52)	+25 (+54)

edly reduced or eliminated in all runs and pools. Shallow-slow portions increased from approximately 30% at normal flows to about 85% with 90% flow reduction. Deep-slow portions remained about the same.

Numbers of Brook Trout in Runs and Pools, 1966–67

The brook trout population age I and older in the test sections generally showed a greater decrease in runs than in pools. During 1966, the reduced flows did not result in noticeable consistent changes in number or weight of trout and the control sections generally changed more than the test sections (Table 2); the numbers of trout in the control and test sections averaged about 23 and 2% less, respectively, and their total weights about 12 and 8% more. In test sections, the greatest decrease of trout occurred in section A run (20%) while decreases in other test sections did not exceed 6%. During 1967, 90% flow reduction resulted in an average decrease of 62% in the number of trout in runs, in comparison with a decrease of about 20% in control runs. Both the number and weight of trout in pools of the test sections generally increased, whereas those in the control pools decreased over 14%. This suggests movement of trout from runs to pools in the test sections.

More underyearling brook trout were taken in runs than in pools in both test and control sections during both years (Table 3), the percentages in runs being 83 for the test sections and 80 for the control sections. The number of underyearling trout general-

TABLE 3. Numbers of underyearling brook trout collected in runs and pools of the various sections at the end of the reduced flow period, 1966 and 1967.

Area	1966	1967
Control, runs	38	19
pools	6	8
Total	44	27
Section A run	42	17
pool	10	5
Section B run	46	44
pool	8	5
Section C run	22	11
pool	7	2
Total	135	84
Runs	110	72
Pools	25	12

TABLE 4. Percentages of tagged trout released in the various sections that were recaptured in various locations after flow reduction during 1966 and 1967.

	1966				1967			
		Recaptures (%)				Recaptures (%)		
	No.[a] tagged	Same place	Same section	Another section	No.[a] tagged	Same place	Same section	Another section
				Section A				
Run	28	7	7	4	17	29	41	0
Pool	20	10	15	0	24	25	42	0
				Section B				
Run	23	30	35	9	17	12	18	23
Pool	37	38	43	3	33	39	45	12
				Section C				
Run	27	44	48	7	36	19	39	11
Pool	33	21	24	3	19	21	32	0
				Control				
Lower								
run	39	26	26	0	28	33	40	0
pool	16	38	38	0	19	27	36	0

[a] Includes trout that were tagged in previous years that were captured and released again.

ly decreased in runs and pools during the study. Flow reductions did not cause the decline because decreases in control and test sections were about equal.

A multiple linear regression was fitted to the 1966 and 1967 data with flow, surface area, average depth, average current velocity, maximum velocity, and cover as the independent variables and number of trout per run or pool as the dependent variable. These six variables accounted ($P = 0.01$) for 77% and 83% of the variation in the number of age I and older trout in runs and pools, respectively. Surface area was the most important variable in pools while flow was the most important in runs. The six variables accounted for 82% ($P = 0.01$) and 68% ($P = 0.05$) of the variation in the number of underyearlings in runs and pools. Flow was the most important variable in both runs and pools.

Recaptures of Marked Trout, 1966–67

In general the number of tagged trout recaptured in the test sections approximated recoveries in the lower control (Table 4) and indicated that reduced flows did not result in noteworthy mortality of trout. During the 1966 flow reduction period 28 dead trout (15 tagged) were recovered on the grates of the lower trap. Seven (1 tagged) were found during 1967. Jaw tagging in 1966 may have caused more mortality than branding in 1967, however, the greater stream velocities in 1966 may have carried more weak or dead fish against the trap.

Movement of tagged trout in the test sections appeared to be similar to movement in the lower control (Table 4). Nearly half of the tag recoveries were made in the same places where the fish were tagged and most of the others were recovered at another location of the same section. Movement of tagged trout from one test section to another was generally quite low. Tag recoveries suggest that trout moved from one run to another or into pools and not from pools to runs. No trout moved out of the test area during 1966. During 1967 over 100 trout entered the upstream trap and none entered the downstream trap. Movement out reached a peak about 10 days after the flow reduction was completed. Most of the trout entering the trap were over 18 cm long.

Discussion

The changes in the physical characteristics measured at various levels of flow reduction were not great. Even at 90% flow reduction the surface area, depth and cover were still considerable, particularly in pools. Average current velocity showed a greater reduction than any other physical characteristic which is consistent with the findings of Curtis (1959). Runs as defined, which may be considered as marginal habitat for catchable size trout with respect to depth and cover, showed a greater percentage reduction in these factors than did pools. The physical characteristics did not change as much as they probably would on many streams because of the well defined stream channel throughout the study area.

Recaptures of marked trout and changes in the standing crop suggest that runs, as marginal habitat for catchable size trout, were more affected than pools. A longer period of reduced flows would probably have a greater effect on the trout population.

Siltation and higher water temperatures could result from reduced flows. Siltation was extensive, especially in Section A, and was caused by the lower current velocity than in the normal stream. Saunders and Smith (1956), stated that low standing crops of brook trout were closely associated with silting, apparently because of the destruction of hiding places. Siltation throughout the summer could also interfere with brook trout reproduction. During 1967, maximum–minimum thermometers at the two ends of the test area did not show a measurable temperature difference. This was probably due to the short distance between them and to ground water accretions.

Movement of trout out of the test sections was recorded in 1967 but not in 1966. The degree of flow reduction in 1966 probably was not sufficient to bring about any emigration. Clothier (1954) reported upstream movement of trout after severe flow reductions in irrigation canals, possibly due to decreased cover and increased competition.

Acknowledgments

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Accumulation of Dieldrin in an Alga (*Scenedesmus obliquus*), *Daphnia magna*, and the Guppy (*Poecilia reticulata*)[1]

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REINERT, R. E. 1972. Accumulation of dieldrin in an alga (*Scenedesmus obliquus*), *Daphnia magna*, and the guppy (*Poecilia reticulata*). J. Fish. Res. Bd. Canada 29: 1413–1418.

Scenedesmus obliquus, *Daphnia magna*, and *Poecilia reticulata* accumulated dieldrin directly from water; average concentration factors (concentration in organism, dry weight, divided by concentration in water) were 1282 for the alga, 13,954 for *D. magna*, and 49,307 (estimated) for the guppy. The amount accumulated by each species at equilibrium (after about 1.5, 3–4, and 18 days, respectively) was directly proportional to the concentration of dieldrin in the water. *Daphnia magna* and guppies accumulated more dieldrin from water than from food that had been exposed to similar concentrations in water. When guppies were fed equal daily rations of *D. magna* containing different concentrations of insecticide, the amounts of dieldrin accumulated by the fish were directly proportional to the concentration in *D. magna*; when two lots of guppies were fed different quantities of *D. magna* (10 and 20 organisms per day) containing identical concentrations of dieldrin, however, the amounts accumulated did not differ substantially.

REINERT, R. E. 1972. Accumulation of dieldrin in an alga (*Scenedesmus obliquus*), *Daphnia magna*, and the guppy (*Poecilia reticulata*). J. Fish. Res. Bd. Canada 29: 1413–1418.

Scenedesmus obliquus, *Daphnia magna* et *Poecilia reticulata* accumulent la dieldrine directement de l'eau. L'indice moyen de concentration (concentration dans l'organisme, poids sec, divisée par celle de l'eau) de l'algue est 1282, celui de *D. magna* 13,954 et celui du guppy 49,307 (estimé). Les quantités accumulées par chaque espèce au point d'équilibre (après environ 1.5, 3 ou 4 et 18 jours respectivement) sont directement proportionnelles à la teneur en dieldrine de l'eau. *Daphnia magna* et les guppys accumulent plus de dieldrine de l'eau qu'à partir d'aliments exposés à des teneurs équivalentes dans l'eau. Pour une portion quotidienne donnée de *D. magna* contenant diverses concentrations d'insecticide, la quantité de dieldrine accumulée par les poissons sont directement proportionnelle à sa teneur dans *D. magna*. Cependant, lorsqu'on donne à deux groupes de guppys des quantités différentes de *D. magna* (10 et 20 organismes par jour) contenant des concentrations identiques de dieldrine, les doses accumulées ne diffèrent pas pour la peine.

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EVIDENCE of the accumulation of chlorinated hydrocarbon insecticides at all trophic levels of the aquatic food chain is well documented (Hickey and Keith 1965; Hunt and Bischoff 1960; Menzie et al. 1965; Rudd 1964; Woodwell 1967; Woodwell et al. 1967). The dynamics of the compounds in aquatic ecosystems are not fully understood, however; they are more complex than in terrestrial ecosystems because organisms may accumulate insecticide by direct uptake from water as well as from food.

The research reported here was designed to study the rate of accumulation of dieldrin from water and food by three organisms from different trophic levels: a green alga *Scenedesmus obliquus;* a cladoceran *Daphnia magna;* and a fish *Poecilia reticulata.*

Materials and Methods

Algae, *D. magna*, and guppies were exposed in the laboratory to different concentrations of dieldrin in water or food. After various periods of exposure, dieldrin was extracted with hexane and quantified by gas chromatography. Extraction efficiencies were determined from the analysis of five samples each of water or organisms to which known amounts of dieldrin had been added.

The dieldrin (Shell Chemical Co., New York 10020) contained not less than 85% 1,2,3,4,10,10-hexachloro-6,7epoxy-1,4,4a,5,6,7,8a-octahydro-1,4-endo-exo-5,8-dimethanonaphthalene. Extraction was with high-purity, glass-distilled chromatographic grade hexane. All other chemicals used were reagent grade.

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CONSTANT FLOW SYSTEM

Mariotte bottles were used to maintain the concentrations of dieldrin in water for experiments with *D. magna* and guppies. The flow rate of 9–10 ml/min completely renewed the dieldrin solution in a 7.4-liter test aquarium about every 12 hr. Mariotte bottles were refilled every 24 hr.

Before introduction of test animals, enough acetone–dieldrin solution was pipetted into the Mariotte bottle to give the desired dieldrin concentrations in the aquarium. Dieldrin concentrations in the aquaria were checked every 12 hr; after concentrations had stabilized, test animals were introduced.

ANALYSIS OF WATER SAMPLES

Water samples for experiments with *D. magna* and guppies were analyzed by extracting 100 ml of water with 15 ml of hexane in a 125-ml separatory funnel. The mixture was shaken 2 min and the hexane layer collected in a 15-ml graduated centrifuge tube for analysis by gas chromatography. Extraction efficiencies were 93–102%.

In the analysis of water containing algae, separation of the water from algae in a Foerst centrifuge preceded extraction with hexane. Extraction efficiencies for these water samples were 64–75%.

ALGAE

The original culture of *Scenedesmus obliquus* was from the Indiana University Collection of Algae; subsequent cultures were grown in 18.5-liter wide-mouth jars in a nutrient medium consisting of 5 g KNO_3, 10 g $M_gSO_4 \cdot 7H_2O$, 5 g KH_2PO_4, and 5 ml Aron A4 micronutrient solution diluted to 1000 ml (Krauss 1953). Two hundred milliliters of this nutrient medium were added to each 18.5-liter stock bottle of algal culture. Compressed air was continuously bubbled through the stock solution. The constant light source for each stock bottle was a desk lamp with a 100-w bulb. Before each experiment the portion of the culture used was filtered through glass wool to remove clumped algae.

In preparing for a test, 200-ml samples of algae were poured into 250-ml Erlenmeyer flasks, stoppered with foam culture stoppers, and gently shaken on a rotary shaker for 24 hr. Dieldrin (0.20, 1.0, and 4.0 μg, to yield concentrations of 1, 5, and 20 ppb), dissolved in 0.5-ml portions of acetone, was then added to the flasks and shaking was continued during the 36-hr period in which samples were collected. The temperature of the cultures during the tests was 24–26 C.

Samples were collected by concentrating algae in a Foerst centrifuge. Five sets of three samples each were collected from each flask — one set just before the addition of dieldrin and the others 8, 16, 24, and 36 hr later. The algae were rinsed in the centrifuge with 250 ml of distilled water, collected on VM-100 Metricel filters of known weight, and dried to constant weight. After the samples were weighed, the filter paper and algae were ground with mortar and pestle with 1 g of sand. The mixture was transferred to a flask containing 10 ml of hexane and shaken 10 min on a rotary shaker; the extract was then decanted into a 50-ml Erlenmeyer flask. The extraction was repeated and the second extract combined with the first. Before analysis on the gas chromatograph, 12 ml of the combined hexane extract were concentrated to 1 ml on a water bath. The concentrate was washed through a glass column (11 mm ID × 20.23 cm long, containing 500 mg of a 1:1 mixture of magnesium oxide and celite) with five 1-ml portions of hexane. Extraction efficiencies were 93–96%.

DAPHNIA

Daphnia magna were cultured in 92.5-liter aquaria and fed dried yeast and algae. Accumulation of dieldrin from water was tested by placing about 700 organisms in each of three 7.4-liter test aquaria containing concentrations of 2.1, 4.5, and 12.5 ppb of dieldrin in water. The concentrations remained nearly stable throughout the 6 days of the experiment. Since *D. magna* reproduced during the experiment, only large adults that were originally introduced into the test aquaria were selected for analysis. *Daphnia magna* were not fed during the tests. Water temperatures in the test aquaria were 20–22 C.

Samples of *D. magna* were collected daily from each test aquarium, rinsed in water, dried to constant weight, and stored in glass vials in a refrigerator. Dried *D. magna* in 5-mg portions (20–28 individuals) were ground with 1 g of sand with mortar and pestle. The pulverized *D. magna* and sand were transferred to a flask and extracted with 5 ml of hexane for 10 min on a rotary shaker. The extract was decanted into a 50-ml Erlenmeyer flask, the extraction repeated, and the second extract combined with the first. No clean-up procedure was needed. Extraction efficiencies were 95–98%.

In one test *Daphnia* were exposed to dieldrin in water that contained algae; 16,000 ml of filtered algal stock culture were poured into an 18.5-liter wide-mouth jar, and 0.5 ml of acetone containing 95 μg of dieldrin was added. Enough compressed air was bubbled through the jar to keep algae suspended. Five days after the addition of the dieldrin, about 2000 adult *D. magna* were placed in the jar. Algae, water, and *D. magna* were sampled periodically throughout the experiment. Concentrations of dieldrin in water were 2.2–4.4 ppb; concentrations in the algae were 4.2–7.5 ppm. Samples were analyzed as previously described.

Guppy food containing known concentrations of dieldrin was produced by exposing *D. magna* to dieldrin. Organisms held for 4 days in aquaria containing concentrations of 1.7–2.4 and 9.8–11.2 ppb dieldrin accumulated concentrations of 32 and 144 ppm, respectively (averages for five samples each; ranges, 29–35 and 139–149). *Daphnia magna* were dried on filter paper and stored in glass vials until used.

FISH

After female guppies were held at laboratory conditions for a minimum of 5 days, 16 (weight range, 0.37 to 0.56 g) were placed in each of three 7.4-liter aquaria containing initial dieldrin concentrations of 0.8, 2.3, and 4.2 ppb. The dieldrin concentrations in water changed slightly during the period of exposure. In the aquarium containing 0.8 ppb the concentration increased slowly throughout the experiment to 1.1 ppb on day 32, but decreased in the other aquaria from 2.3 and 4.2 ppb to lows of 1.4 and 2.1 ppb, respectively, 4 days after introduction of the fish. During the next 14 days the concentrations gradually increased to levels near the initial values. Fish were fed live, dieldrin-free *D. magna;* those not eaten within 5 min were removed from the tank. There was no detectable concentration of dieldrin by *D. magna* during the 5-min exposure. Water temperatures were 20–22 C.

Two fish were removed from each aquarium for analysis on predetermined days. Each was weighed, homogenized in a Corning glass tissue grinder, and washed into a 50-ml Erlenmeyer flask with four 5-ml portions of alcoholic KOH (5 g KOH dissolved in 3 ml water and diluted to a volume of 20 ml with absolute alcohol). The flask was heated on a water bath for 15 min. After cooling, the contents were transferred to a 125-ml separatory funnel. The flask was rinsed with 10 ml of distilled water and the rinse added to the contents of the separatory funnel. The alcoholic KOH was extracted three times with 10-ml portions of hexane. No clean-up procedure was needed. Extraction efficiencies were 94–101%.

In feeding experiments, individual guppies kept in 3.7-liter wide-mouth jars were fed daily rations of 10 and 20 *D. magna* containing an average of either 32 or 144 ppm dieldrin. This ration amounted to about 2 and 4% of the body weight of the fish, on a dry-weight basis. Fish ate all *Daphnia* they were fed.

Gas Chromatography

Dieldrin concentrations in hexane extracts were measured with a model 400 F & M gas chromatograph equipped with an electron capture detector. Before analysis, extracts were diluted or concentrated on a water bath to a volume that would bring a 5-μliter injection within the linear range of the electron capture detector. The carrier and purge gas contained 95% argon and 5% methane. Constant rates of flow were maintained at 70 ml/min for the carrier and 50 ml/min for the purge gas. Operating temperatures were 185 C for the column oven, 200 C for the detector, and 240 C for the flash heater. The "U" column was a 122-cm section of 4-mm ID glass tubing. Column packing was a diaport S support material of 80/100 mesh, coated with 3.8% SE-30 silicone gum rubber.

Results

All organisms tested accumulated dieldrin from water during an initial period of exposure, until a nearly stable equilibrium was attained. The amounts accumulated were directly proportional to the amounts in the water.

Algae exposed to initial concentrations of 1, 5, and 20 ppb of dieldrin accumulated 1.3, 7.1, and 25.2 ppm after 36 hr of exposure (Fig. 1); concentrations appeared to reach equilibrium at a point between 24 and 36 hr. *Daphnia magna* exposed to initial concentrations of 2.1 and 4.5 ppb dieldrin accumulated 35 and 62 ppm after 3 days; concentrations changed little during the next 3 days (Fig. 2a, b). *Daphnia magna* exposed to an initial level of 12.8 ppb accumulated a maximum of 184 ppm on the fourth day; concentrations then changed little during the remaining 2 days (Fig. 2c). In guppies exposed to initial dieldrin concentrations of 0.8, 2.3, and 4.2 ppb, the amounts accumulated gener-

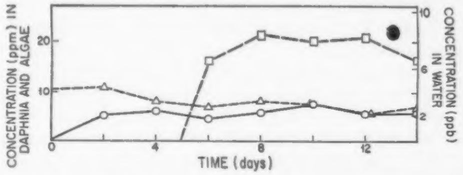

Fig. 1. Dieldrin concentrations in algae after exposure for 36 hr to three concentrations in water. Values are averages for three samples; horizontal lines above and below each average value show the range.

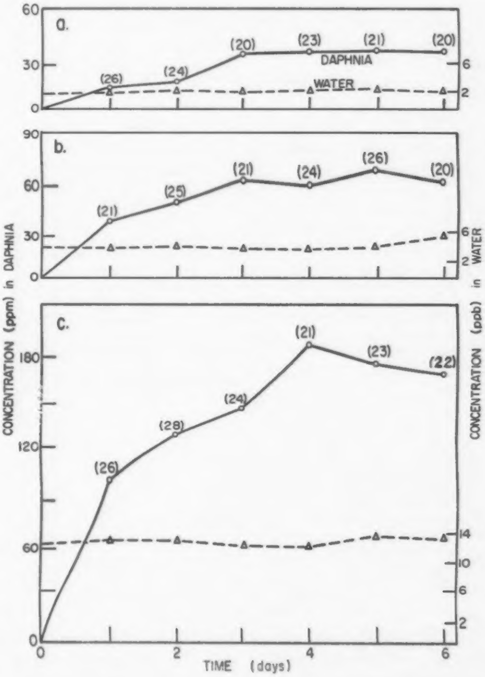

Fig. 2. Concentrations of dieldrin in *D. magna* exposed to initial concentrations in water of 2.1 ppb (a), 4.2 ppb (b), and 12.8 ppb (c). The numbers of *D. magna* in each sample are shown in parentheses.

ally rose steadily during the first 17 days, and then tended to stabilize during the following 15 days (Fig. 3).

It was not possible to determine how much of the insecticide accumulated by the organisms, particularly algae, was absorbed and how much was simply adsorbed to the outer surface of the organisms. Although samples of algae were rinsed with distilled water before extraction, it is possible that a portion of the dieldrin was adsorbed. Analysis of exuvia of *D. magna* and of hexane rinses of guppies showed no detectable amounts of dieldrin, however, suggesting that most of the insecticide was absorbed by these organisms.

Dieldrin concentration factors (concentration in organism divided by concentration in water) differed greatly between species (Fig. 4). When equilibrium was reached between concentrations in water and in the organisms, average concentration factors for dry weight samples were 1282 for algae, 13,954 for *D. magna*, and 49,307 (estimated) for guppies. Concentration factors for guppies were originally calculated on a wet-weight basis (Fig. 4); since the fish contained 71–76% (average, 74%) water, the concentration factor for dry-weight samples was estimated to be 3.88 times greater than that for wet-weight values. Thus, on a dry-weight basis, the dieldrin concentrations attributed to direct uptake from water were about 10-fold greater in *D. magna* than in algae, and about 3½-fold greater in guppies than in *D. magna*.

The concentration factors for algae may be slightly (but not substantially) higher than shown in Fig. 4 because the dieldrin concentrations in water were calculated from the amount added to the water rather than the amount in it. Neither the dieldrin lost from the water through accumulation by the algae nor that probably lost through codistillation with evaporating water and adsorption to the sides of the glass containers was taken into consideration. Since analyses of dieldrin in the water containing algae showed concentrations to be 44–88% of the amount

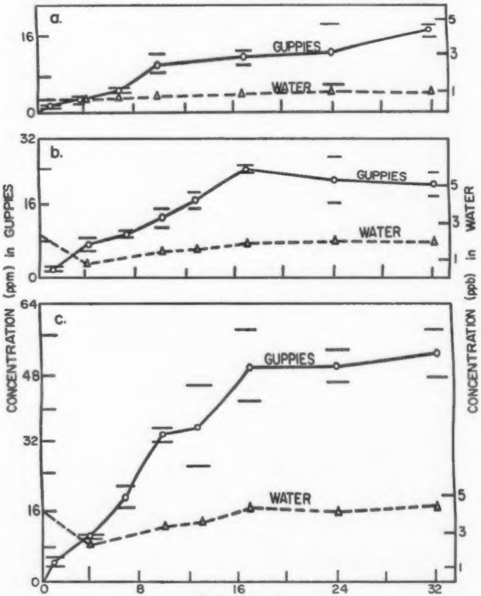

FIG. 3. Dieldrin concentrations in water and guppies during a 32-day exposure to water having concentrations of 0.8–1.1 ppb (a), 0.8–2.3 ppb (b), and 2.1–4.3 ppb (c). Plotted points for fish are averages for two specimens; horizontal lines above and below each average value show the individual values.

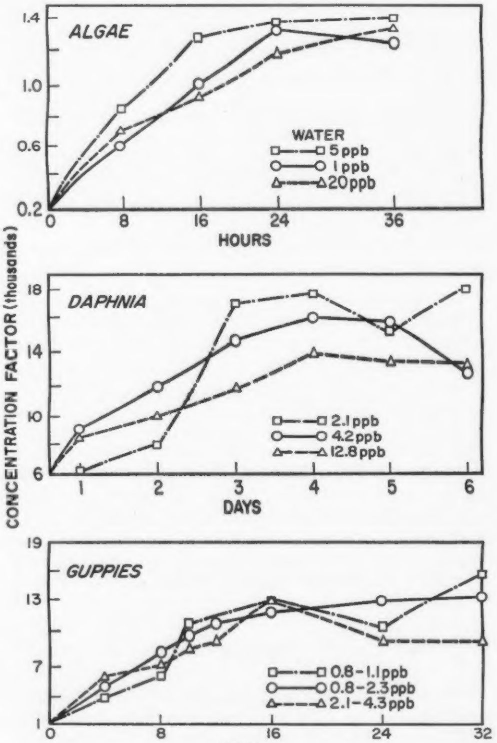

FIG. 4. Concentration factors for algae, *D. magna* and guppies exposed to different concentrations of dieldrin in water. Concentration factors for algae and *D. magna* were calculated on a dry-weight basis and those for guppies on a wet-weight basis.

added, however, the error could not have been large enough to affect appreciably the general relation shown here between the concentrations in algae, *D. magna*, and guppies.

Daphnia magna accumulated slightly more dieldrin from water containing 2.1–2.8 ppb than from a combination of water containing 2.2 to about 3 ppb and algae containing 4.2–7.5 ppm (Fig. 5). Feeding by *D. magna* was verified by the presence of algal cells in the digestive tract. There is no obvious reason for the greater accumulation from water alone than from water plus food, since *D. magna* for both experiments were from the same population and the experiments were run simultaneously. Whatever the reason, the data suggest that, under the conditions of these experiments, the water was the principal source for the concentration of dieldrin by *D. magna*.

Guppies in dieldrin-free water accumulated insecticide when they were fed dried *D. magna* contaminated with dieldrin. Fish fed *D. magna* containing an average of 32 or 144 ppm dieldrin, at the same rate (10 per day), accumulated concentrations that were proportional to the levels in the food (Fig. 6). The concentrations of insecticide were similar, however, in guppies fed *D. magna* containing 32 ppm dieldrin at different rates (10 and 20 per day; Fig. 7).

Guppies held in dieldrin-free water and fed *D. magna* containing an average of 32 ppm dieldrin accumulated less than one tenth as much of the insecticide as guppies held in water containing 0.8–2.3 ppb dieldrin (Fig. 7). Fish fed *D. magna* contaminated with 144 ppm dieldrin accumulated more than 9 ppm in 30 days (Fig. 6). Had these fish been exposed to the same concentration of insecticide in water as that to which the *D. magna* were exposed (9.8–11.2 ppb), they unquestionably would have developed far higher concentrations (e.g. see Fig. 3)

Discussion

The observation that *Daphnia* and guppies accumulated more dieldrin directly from water than from food that had been exposed to about the same concentrations in water confirms observations made in other experiments. Chadwick et al. (1969)

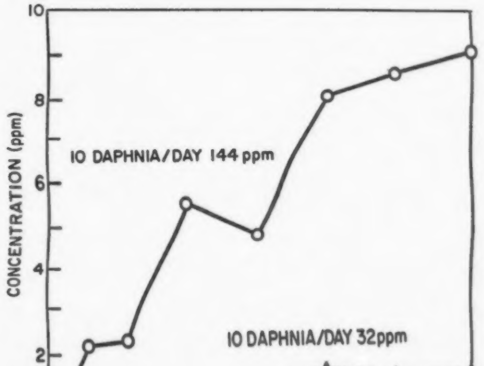

FIG. 5. Dieldrin concentrations in water (△) and in algae (○) and *D. magna* (□) during exposure periods of 14 and 9 days, respectively. *Daphnia magna* were introduced on the fifth day.

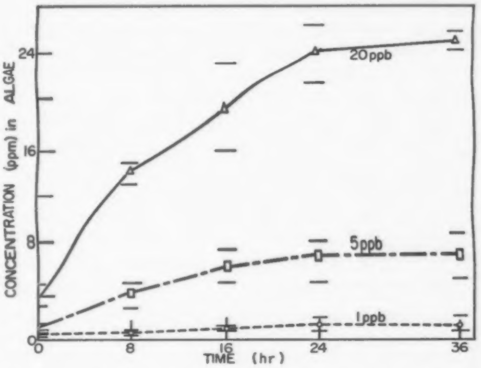

FIG. 6. Dieldrin concentrations in two groups of guppies fed 10 *D. magna* per day containing 32 and 144 ppm of dieldrin. Each point represents the average for two guppies.

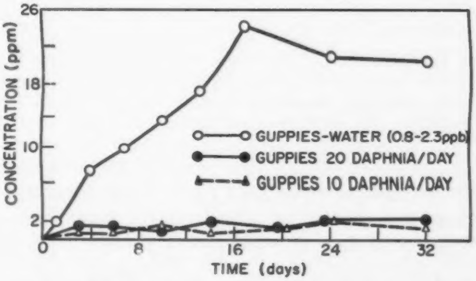

FIG. 7. Dieldrin concentrations in guppies held in water containing 0.8–2.3 ppb dieldrin and in guppies held in dieldrin-free water but fed two quantities of *D. magna* containing an average of 32 ppm dieldrin. Each point represents the average for two fish. These *D. magna* were raised in water with a dieldrin level of 1.8–2.5 ppb.

observed that, when reticulate sculpins (*Cottus perplexus*) were fed midge larvae exposed to the same concentration as the fish, not more than 16% of the dieldrin accumulated by the sculpins could have come from the food. Lenon (MS 1968) observed that the concentrations of dieldrin in bluntnose minnows (*Pimephales notatus*) that were fed *D. magna* exposed to about the same concentration as the fish did not differ significantly from the concentrations in fish exposed only to dieldrin in water. Macek and Korn (1970), on the other hand, reported that brook trout (*Salvelinus fontinalis*) concentrated more *p,p'*DDT from food than from water. In their experiment, however, the concentration of the insecticide was about 1 million times higher in the food (dried pellets) than in the water.

In the present study, the concentration factors for direct accumulation of dieldrin from water increased from algae to *D. magna* to guppies, giving the appearance of accumulation through a simple food chain. Hamelink et al. (1971) observed that, in lentic environments, concentrations of DDT residues increased from one trophic level to the next regardless of whether the residues were primarily accumulated from food or water. He concluded that differences in adsorption and solubility are the prime factors in determining concentrations of chlorinated hydrocarbon compounds in different trophic levels of aquatic ecosystems.

Although the present study demonstrates that direct accumulation of insecticides from water can contribute significantly to the total concentrations accumulated by aquatic organisms, two important factors not investigated here influence the degree to which accumulation from water contributes to the amount of insecticide concentrated: (1) Water contains varying amounts of organic and inorganic materials to which substantial amounts of chlorinated hydrocarbon insecticides may be bound and held unavailable for direct accumulation from water (consequently, concentrations calculated from unfiltered extracts of water samples may not always be a reliable indication of the amount of insecticide available for direct accumulation). (2) Not all organisms in natural aquatic systems are exposed to the same concentrations of insecticides. Sediments, for example, often contain much higher concentrations than the water. Consequently, invertebrates that live or feed in sediments may enter the food chain containing much higher concentrations than if they had been exposed only to the amount in the water. The interaction of these factors, and chemical and biological variability among bodies of water, make it extremely difficult to predict, solely from a knowledge of the concentration in water, the amounts of insecticides that fish and other aquatic organisms will accumulate.

Acknowledgments

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Sound-Scattering Layers in the Northeastern Pacific

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DONALDSON, H. A., AND W. G. PEARCY. 1972. Sound-scattering layers in the northeastern Pacific. J. Fish. Res. Bd. Canada 29: 1419–1423.

Temporal and spatial variations in the depth, thickness, and vertical movement of scattering layers were studied using a 38.5 kHz echosounder in waters off Oregon and between Hawaii and Adak, Alaska.

Off Oregon one or two layers migrated toward the surface at dusk and descended into deeper water at dawn. Although individual scattering layers migrated at a fairly constant rate during a twilight period, rates of ascent and descent varied from day to day. Average rates were 2–3 m/min. During the night the depth of the top of the scattering layer averaged 40 m, and it varied between 50–245 m during the day. The bottom of the deepest recorded layer was 450 m deep.

Regardless of intensity, the thickness of the scattering layers in the water column was usually greater during night than day. It was greater over the continental slope than abyssal depth, and in some years it was greater during the summer than during other seasons.

Between Hawaii and Adak, Alaska, central waters had large amounts of scattering but low midwater trawl catches, transitional waters had high-intensity scattering layers and high biomass, and subarctic waters had very reduced scattering layers but high biomass.

DONALDSON, H. A., AND W. G. PEARCY. 1972. Sound-scattering layers in the northeastern Pacific. J. Fish. Res. Bd. Canada 29: 1419–1423.

Nous avons étudié les variations temporelles et spatiales de la profondeur, de l'épaisseur et des déplacements verticaux des couches diffusantes au large de l'Orégon et entre Hawaii et Adak, Alaska. Nous avons utilisé à cette fin un sondeur à écho de 38.5 kHz.

Au large de l'Orégon, une ou deux couches diffusantes remontent vers la surface au crépuscule et retournent en profondeur à l'aube. Quoique les couches individuelles se déplacent à une vitesse relativement constante pendant une période de demi-jour, le rythme de montée et de descente varie de jour en jour. La vitesse moyenne est 2–3 m/min. La profondeur de la partie supérieure de la couche diffusante est de 40 m en moyenne la nuit, et elle varie de 50–245 m le jour. Le niveau inférieur de la couche la plus profonde a été enregistré à 450 m. Indépendamment de l'intensité, les couches diffusantes dans la colonne d'eau sont ordinairement plus épaisses la nuit que le jour. Elles sont plus épaisses sur la plate-forme continentale que dans la zone abyssale et, certaines années, plus épaisses en été qu'en toute autre saison.

Lors d'une croisière entre Hawaii et Adak, Alaska, nous avons observé un haut degré de diffusion, mais de faibles captures du chalut semi-pélagique dans les eaux centrales, des couches diffusantes de haute intensité et une biomasse abondante dans les eaux de transition, et des couches très réduites, mais à biomasse abondante, dans les eaux subarctiques.

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SINCE World War II, sound-scattering layers have been discovered in midwater regions of most of the world's oceans. Many studies have been aimed at determining the cause of scattering, but few have examined seasonal and spatial variations in one region.

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Organisms suggested as causes of scattering include squids (Lyman 1948), euphausiids (Moore 1950), fishes (Marshall 1951; Johnson et al. 1956; Backus and Barnes 1957; and Taylor 1968), and siphonophores (Barham 1963). Tucker (1951), Kampa and Boden (1954), and Barham (MS 1956, 1966) suggested that scattering may be caused by more than one group of organisms. The few seasonal studies of scattering layers are those by Barham (MS 1956) in Monterey Bay, California, and Hunkins (1965) from Fletcher's Ice Island.

The migrations of scattering layers and the changes in scattering from day to night, from season to season, and from inshore to offshore were studied off the Oregon coast over a period of several years. The relations of scattering to the biomass of various groups of animals were investigated on a cruise between Hawaii and Adak, Alaska.

Materials and Methods

Most of this study was made at stations 25 and 50 nautical miles off Newport, Oregon. The 25-mile station is located over the outer continental shelf, and the 50-mile station is at the outer edge of the continental slope in oceanic waters. Observations were also made on a cruise between Hawaii and Adak, Alaska.

To detect scattering layers a model 510-5 Simrad Echosounder, operated at a frequency of 38.5 kHz, was used. From January 1963 to September 1964, echotraces were recorded aboard the R/V *Acona* using a pulse length of 2.4 m/sec, an amplification of about 54 db, and a gain reduction in the surface waters. After September, 1964, echotraces were taken aboard the R/V *Yaquina* where the setting on the echosounder was the same except for a slightly lower amplification (about 6 db lower).

To examine possible relations of scattering to the biomass of various groups of organisms between Hawaii and Adak, Alaska, animals were collected with a 6-ft Isaacs–Kidd midwater trawl (with a 5-mm square measure mesh liner). The trawl did not sample specific layers but was towed obliquely from 0–200 m at night. The echosounder was operated continuously while sampling was underway.

Results

VERTICAL MIGRATION OF SCATTERING LAYERS

The vertical migration of scattering layers off Oregon consisted of the typical descent into deep water at dawn and ascent at dusk. During ascent and descent one or two layers were observed to migrate.

The average rates and standard deviations are 2.4 ± 0.8 m/min for descent and 3.1 ± 0.8 m/min for ascent. The rates at which single layers migrated generally remained fairly constant. However, in some instances when two layers ascended, the lower sometimes migrated at an increasing rate. In one case the ascent of the lower layer slowed as the night depth was reached. Although Bary (1967) distinguished four stages of migration based on changes in the rate of movement and the appearance of layers during migration, similar stages were usually not apparent in our study.

DAY-NIGHT SCATTERING

Several series of echosoundings were made at one station for periods of 10–48 hr to observe differences in the vertical position of the layers and changes in the thickness of scattering in the water column.

As expected, the main scattering layers were deeper during the day than the night (Fig. 1A and B). Excluding surface scattering, the average depths and standard deviations for upper layers (measured from the surface to the upper edge of scattering) were 40 ± 14 m at night and 180 ± 52 m during the day. The maximum depth of a recorded scattering layer (measured to the lower edge of scattering) was 450 m.

Generally, the total thickness of scattering layers, regardless of intensity, was greater during night (140 ± 57 m) than day (109 ± 66 m) (Fig. 1B). In other echograms, day and night intensities and amounts of scattering were similar (Fig. 1A).

The observed greater thickness of scattering layers at night could be due to their proximity to the echosounder or to the spreading of the layers at night in the absence of light intensities to which the organisms are adapted during the day. The spreading of the layers at night is supported by Taylor (1968), who caught fewer fishes in scattering layers during the night than during the day.

INSHORE-OFFSHORE VARIATIONS IN SCATTERING

Intense scattering was often present during the night from the surface to the bottom over the continental shelf (Fig. 1C, station 15 miles from shore). Near submerged banks the midwater scattering layer was often penetrated by the bank while in other areas dense clouds of scattering (possibly rockfishes, *Sebastodes* spp.) on the top of the banks corresponded with a gap in the overlying, midwater scattering layer (Fig. 1E). Isaacs and Schwartzlose (1965) suggested that a similar gap was caused by the feeding of predators from the bank on the midwater scattering layer.

In waters beyond the slope the maximum thickness of scattering in the water column was often found within 45 miles of shore and decreased in an offshore direction (Fig. 1D). A maximum in the biomass of fishes, squids, and shrimps 45 miles offshore (Pearcy unpublished) suggests a general correlation between biomass of small nekton and scattering off Oregon.

SEASONAL VARIATIONS IN SCATTERING

Seasonal variations in the thickness and intensity of scattering layers were examined in night echograms at the station 50 miles offshore. In 1963, the amount of scattering was lowest in the winter

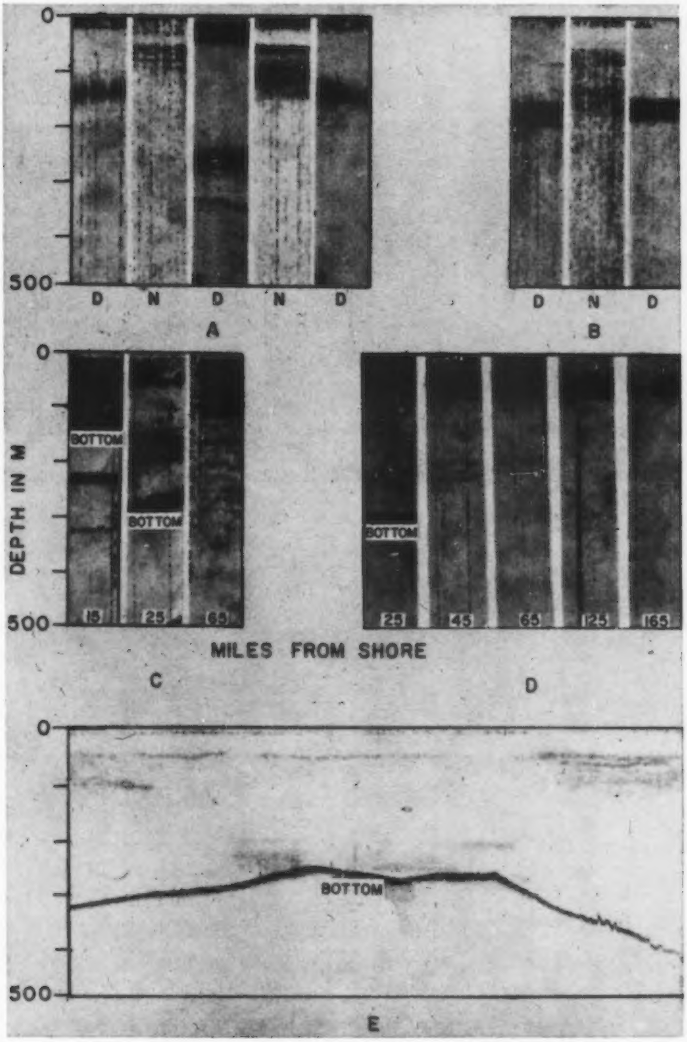

FIG. 1. (A–B) Day versus night differences in scattering 50 miles from Newport, Oreg. (C–D) Inshore to offshore variations in scattering off Newport, Oreg. (E) Scattering layers near a submerged bank off Newport, Oreg.

Donaldson and Pearcy — J. Fish. Res. Bd. Canada

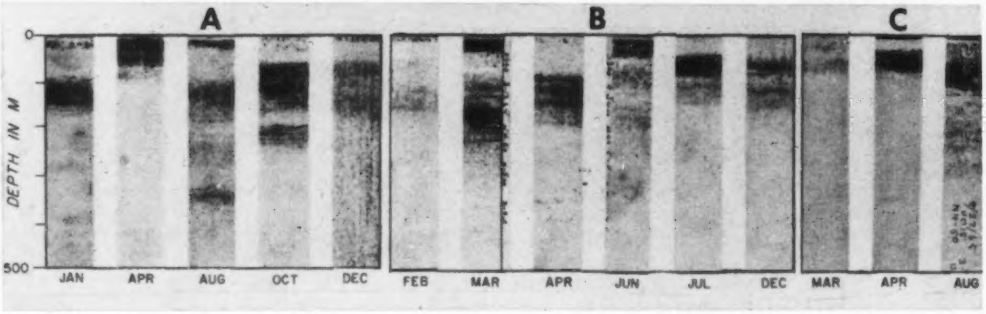

FIG. 2. (A–C) Seasonal variations in nighttime scattering 50 miles from Newport, Oreg. in 1963 (A), 1964 (B), and 1965 (C).

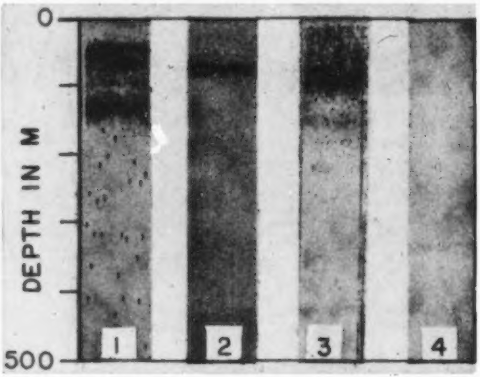

FIG. 3. Geographic variations in scattering between Hawaii and Adak, Alaska.

Donaldson and Pearcy — J.Fish. Res. Bd. Canada

TABLE 1. Relationship of scattering to biomass of various groups between Hawaii and Adak, Alaska (Sampling device: 6-ft midwater trawl).

Trace No. in FIG. 3.	Date	Position	% of the water column sampled by the trawl and occupied by scattering	Plankton total (g wet wt/10^3 m^3 taken in the 6-ft trawl	Ratio of euphausiids to the other abundant plankters indicated	Fish biomass g dry wt/10^3 m^3	Shrimp biomass g dry wt/10^3 m^3	Squid biomass g dry wt/10^3 m^3
1	June 1, 1966	25°46.2′N 160°17.3′W	50	4.23	4:1 Jellies[1]	0.43	0.11	0.05
2	June 12, 1966	33°33′N 164°21.6′W	25	28.70	1:4 Copepods	2.56	0.70	0.64
3	June 16, 1966	42°35.5′N 171°02.8′W	75	35.55	2:3 Jellies[1]	16.63	3.08	1.85
4	June 22, 1966	50°29.0′N 176°04.0′W	0.5	64.40	4:1 Jellies[1]	3.32	0.50	1.15

[1] Jellies includes: salps, ctenophores, and medusae.

and spring and highest in the summer and fall (Fig. 2A). The total thickness of scattering was directly related to the number of reverberation layers. Most scattering occurred in the summer when four reverberation layers were present. In 1964, scattering was quite variable. Moderately thick layers were present during spring, summer, and winter (Fig. 2B). During July, the layers were not as thick but scattering intensity was high. These narrow, high-intensity layers may indicate a density of scattering agents equal to that of broad low-intensity layers, thus making evaluation of seasonal variations difficult. The data for 1965 were limited, but again indicated less scattering during the spring than during the summer (Fig. 2C).

MID-PACIFIC OBSERVATIONS

On the cruise from Hawaii to Adak, Alaska, differences in scattering were related to water mass types and biomass. The scattering layers typical of North Pacific central water are shown in Figure 3, Traces 1 and 2. In the southern portion of this water mass, well developed reverberation layers were present (Fig. 3, Trace 1); but, farther north, scattering was less evident and occurred only as a single layer (Fig. 3, Trace 2). Also, in the southern portion of the water mass, plankton biomass was low and euphausiids were the dominant animals (Table 1, Trace 1). Towards the northern half of the water mass, plankton biomass increased notably and the dominant organisms changed from euphausiids to copepods (Table 1, Trace 2). The decrease in scattering is associated with this change in dominant organism.

The transition region between central and subarctic water masses was characterized by an increase in scattering (Fig. 3, Trace 3) and biomass of all groups (Table 1, Trace 3). Biomass of shrimps, fishes, and squids were largest here, and plankton biomass was much larger than in central water.

North of the transition zone, the Pacific subarctic water mass was characterized by the virtual absence of scattering (Fig. 3, Trace 4). Nevertheless, catches contained the highest plankton biomass, composed primarily of euphausiids (Table 1, Trace 4), a lower biomass of fishes than that found in the transition region but higher than that in central water, and a biomass of shrimps and squids comparable to that found in central water.

In summary, the central water mass had a large percent of the water column sampled by the trawl occupied by scattering but a low biomass of plankton, fishes, shrimps, and squids. Euphausiids predominated where scattering was at a maximum. The transitional region had a large biomass of all groups and a large amount of scattering. The subarctic water mass had almost no scattering but high biomass of most groups including euphausiids. These results indicate the difficulty in correlating scattering and biomass where different ocean environments are sampled. Undoubtedly, more consistent results would be obtained with discrete depth sampling and an analysis of species and their scattering properties.

Discussion

Variability was the most striking feature of the scattering off Oregon. The extent of migration of the layers, the thickness of scattering layers present over a diel period, and the thickness of scattering present during different months all fluctuated. This variability may have several causes: differences in acoustical scattering associated with differences in species composition; changes in distribution, behavior, and morphology of life stages of organisms; patchiness in the distributions of organisms; differential attenuation of sound; and variable reactions of scattering organisms to physical conditions such as ambient light.

Although no marked seasonal changes in species composition of midwater fishes were observed off Oregon (Pearcy 1964), seasonal changes in number or biomass occur and may lead to seasonal differences in scattering. Pearcy and Laurs (1966) caught larger numbers of mesopelagic fishes during June–October than during the remainder of the year at the station 50 miles from shore, the same station where we studied seasonal variations of scattering. The biomass of small nektonic animals (fishes, squids, and shrimps) was also larger during the summer than the winter over the continental slope (Pearcy unpublished). In another study, Hebard (MS 1966) found larger populations of *Euphausia pacifica* through the summer and fall of 1963 than in the winter of 1964 at a station 45 miles from shore.

Patchy distribution of organisms may influence scattering at one location, particularly if observations are several hours apart. At the same location where the scattering layers were monitored, Pearcy (1964) found clumped distributions of four species of mesopelagic fishes. Patchiness was not apparent from echo-traces, however. Layers appeared continuous when the vessel steamed between stations or was adrift, suggesting that the volume of water from which scattering was dectected was greater than the patch size of animals.

Acknowledgments

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Inadequacy of Aquarium Antibacterial Formulations for the Inhibition of Potential Pathogens of Freshwater Fish

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Trust, T. J. 1972. Inadequacy of aquarium antibacterial formulations for the inhibition of potential pathogens of freshwater fish. J. Fish. Res. Bd. Canada 29: 1425–1430.

The antibacterial activity of fourteen products marketed for the therapy and prophylaxis of bacterial infections of aquarium fishes was tested. When used at the dilution recommended by the manufacturers, the products failed to inhibit the growth of bacterial species known to be potential pathogens of freshwater fishes and failed to reduce significantly the bacterial numbers in water containing fish. Concentrations of the products that were bacteriostatic, bactericidal, or sporicidal were markedly higher than the recommended concentrations. Use of the products at higher concentrations in aquaria showed two of the products to be inimical to fish.

Trust, T. J. 1972. Inadequacy of aquarium antibacterial formulations for the inhibition of potential pathogens of freshwater fish. J. Fish. Res. Bd. Canada 29: 1425–1430.

L'auteur évalue le pouvoir antibactérien de quatorze produits commerciaux thérapeutiques et prophylactiques contre les infections bactériennes des poissons d'aquarium. Aux dilutions recommandées par les manufacturiers, ces produits ne limitent pas la croissance de bactéries reconnues comme pathogènes en puissance des poissons d'eau douce, et n'entraînent pas une diminution sensible du nombre de bactéries de l'eau contenant les poissons. Les concentrations bactériostatiques, bactéricides ou sporicides sont beaucoup plus élevées que celles recommandées. L'emploi en aquarium de concentrations plus élevées que celles recommandées démontre que deux de ces produits sont mauvais pour les poissons.

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Many species of warmwater tropical fishes are sold to hobbyists for home aquaria and are also used extensively in a number of areas of biological research (Nigrelli 1953). These aquarium fishes are susceptible to bacterial infections and the most frequently encountered bacterial diseases are fin and tail rot, furunculosis, gill infections, piscine mycobacteriosis, columnaris disease, and infectious hemmorhagic septicemia (Bullock et al. 1971, Van Duijn 1967). A number of products are manufactured and marketed for the therapy and prophylaxis of these diseases. In the course of other studies on the use of antibacterial agents in fish culture it was necessary to ascertain the effectiveness of these formulations against a number of species of bacteria known to be pathogenic for fishes. This paper reports on the antibacterial activity of fourteen of these formulations as determined by standard bacteriological assay methods and by bioassay.

Materials and Methods

Products Tested

The fourteen liquid formulations tested were purchased from commercial outlets in Victoria, B.C. The products were produced by five manufacturers in Canada, England, West Germany, and the United States for the therapy and prophylaxis of bacterial infections of aquarium fishes.[a] Products 1, 3, 6, 9, 10, 11, and 14 were also formulated (manufacturers' promotion literature) to treat infections caused by molds. Product 4 was an antiseptic cleanser for use in cleaning aquaria. This product contained an unspecified quaternary ammonium compound at an unspecified concentration. The active ingredients of products 1, 2, 3, and 6 were not provided by the manufacturers. The active ingredients of product 5 were sulfanilamide (16.7 g/liter) and sulfamethazine (5.2 g/liter). Product 7 contained unspecified concentrations of 6,9 diamino-2-ethoxyacridine lactate, 3,6-diamino-10-methyl acridinium chloride, 9 aminoacridine hydrochloride, formaldehyde, and methylene blue. Product 8 contained sulfathiazole (0.0075 g/liter) and quinine sulfate (0.015 g/liter). Product 9 contained neutral acriflavine (0.45 g/liter) and methylene blue (0.074 g/liter), and product 10 contained methylene blue (12 g/liter). The active ingredient of product 11 was malachite green (7.5 g/liter). Product 12 contained sodium sulfathiazole (0.0075 g/liter). Product 13 contained $KMnO_4$ (2 g/liter), and product 14 contained Ag_2O at an unspecified concentration. The concentration recommended by the manufacturers for the use of each product is shown in Table 1.

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[a] The market name of the product and the manufacturer are listed in the laboratory protocol.

TABLE 1. Bacteriostatic activity of aquarium aids.

Product tested	Manufacturers recommended usage dilution	Dilution of products inhibiting bacterial growth[a]							
		A. liquefaciens 14715[b]	*A. salmonicida* 14174	*B. subtilis* 6057 (spores)	*C. columnaris* 23463	*M. marinum* 927	*P. aeruginosa* 15442	*P. putida* 12633	*S. aureus* 6538
1	1:3500	1:400	1:200	1:100	1:40	1:20	1:100	1:200	1:20
2	1:10,000	1:80	1:400	1:80	1:80	<1:2	1:2	1:4	1:80
3	1:10,000	1:100	1:200	1:100	1:100	1:200	1:100	1:200	1:100
4	–[c]	1:8	1:20	1:20	1:80	1:2	1:4	1:8	1:100
5	1:5500	<1:2	<1:2	<1:2	<1:2	<1:2	<1:2	<1:2	1:2
6	1:1100	1:16	1:4	1:4	1:4	1:4	1:8	1:8	1:10
7	1:2000	1:100	1:100	1:400	1:80	1:80	1:40	1:40	1:100
8	1:900	<1:2	1:2	<1:2	<1:2	<1:2	<1:2	<1:2	<1:2
9	1:300	1:16	1:20	1:100	<1:2	1:20	<1:2	1:4	1:40
10	1:2000	1:80	1:100	1:80	1:100	<1:2	1:2	1:4	1:100
11	1:90,000	1:800	1:1000	1:16	1:800	1:2	1:6	1:200	1:2000
12	1:800	<1:2	<1:2	<1:2	<1:2	<1:2	<1:2	<1:2	<1:2
13	1:1800	<1:2	1:2	<1:2	1:2	1:4	<1:2	<1:2	<1:2
14	1:15,000	1:2	1:2	1:2	1:2	<1:2	<1:2	1:2	<1:2
Phenol	–	1:400	1:1000	1:400	1:200	1:1000	1:800	1:800	1:400

[a] Final dilution (v/v) of product in culture broth (not based on active ingredients).
[b] American Type Culture Collection number.
[c] Usage dilution not specified by manufacturer.

TEST ORGANISMS

Aeromonas liquefaciens American Type Culture Collection (1970) 14715, *Aeromonas salmonicida* ATCC 14174, *Chondrococcus columnaris* ATCC 23463, *Mycobacterium marinum* ATCC 927, and *Pseudomonas putida* ATCC 12633 were selected for study because these species cause infection in aquarium fishes (Bullock et al. 1971). *Pseudomonas putida*, *M. marinum*, and species of *Aeromonas* have also been isolated from a variety of clinical diseases in man (Adams et al. 1970, Janssen 1970, Von Graevinitz and Weinstein 1971). *Pseudomonas aeruginosa* ATCC 15442 and *Staphylococcus aureus* ATCC 6538 were chosen for study because these species are those recommended by the Association of Official Analytical Chemists (1970) for disinfectant testing. These species are also human pathogens (Wilson and Miles 1964). *Bacillus subtilis* ATCC 6051 was chosen because of its ability to form spores and because *Bacillus* species are common in fish feeds (Trust and Money 1972). A spore suspension was used in assays.

PREPARATION OF INOCULUMS

Different cultural conditions were required to prepare inoculums of the test species for the antibacterial assays. Cultures of *P. aeruginosa* and *S. aureus* were incubated at 37 C for 24 hr in Trypticase Soy broth (Baltimore Biological Laboratories), while *A. liquefaciens* and *P. putida* were incubated at 30 C for 24 hr. *Aeromonas salmonicida* was grown in Brain Heart Infusion broth (BBL) at 30 C for 24 hr. *Mycobacterium marinum* was grown on Trypticase Soy agar slants (BBL) at 30 C for 48 hr and the growth on one slant was suspended in 5 ml of Trypticase Soy broth. *Chondrococcus columnaris* was grown as 5 ml stab cultures in 0.25% (w/v) Tryptone (Difco) with 0.9% (w/v) agar (Difco). The cultures were incubated at 30 C for 48 hr, and the growth from one stab culture suspended in 5 ml of Brain Heart Infusion broth. The *B. subtilis* spore suspension was prepared by the method of the Association of Official Analytical Chemists (1970). This suspension contained 8×10^7 viable spores per ml.

These cultures were then used to assay the bacteriostatic and bactericidal properties of the test formulations.

BACTERIOSTATIC ACTIVITY OF PRODUCTS

The dilution of each test product which prevented the growth of each test species was determined by serial tube dilution using the method described by Kavanagh (1963). Duplicate twofold dilutions of the test product were prepared in broth. Mueller–Hinton broth (BBL) was used for assays of products containing sulfonamides (Products 5, 8, and 12), and Brain Heart Infusion broth was used for assays of *A. salmonicida* and *C. columnaris*. Trypticase Soy broth was used for all other assays. Each dilution was then inoculated with 0.03 ml of the appropriate inoculum culture (containing approximately 10^9 viable cells per ml), and incubated at 30 C for 96 hr. Assays with *P. aeruginosa* and *S. aureus* were incubated at 37 C for 96 hr. Tubes were then examined for the presence or absence of growth of the test species.

Bactericidal Activity of Products

The Phenol Coefficient–Official Final Action Method of the Association of Official Analytical Chemists (1970) was followed for bactericidal assays. Duplicate dilutions of the test product were prepared in sterile distilled water to a final volume of 5 ml. A 0.5-ml aliquot of the inoculum culture of the test species was added to the medication tube, the tube was agitated gently, and the mixture was incubated at 20 C in a water bath. At intervals of 5, 10, 15, 30, and 60 min after seeding, a 4-mm loopful was transferred from the medication tube to a subculture tube containing 20 ml of growth medium. Assays of product 4 were subcultured to AOAC Letheen broth (BBL) to inactivate any quaternary ammonium compound carried over during subculture. Assays of other Products with *A. salmonicida* and *C. columnaris* were subcultured into Brain Heart Infusion broth. Assays with *A. liquefaciens*, *B. subtilis* spores, *M. marinum*, *P. aeruginosa*, *P. putida*, and *S. aureus* were subcultured into Trypticase Soy broth. The subculture tubes inoculated with *P. aeruginosa* and *S. aureus* were incubated at 37 C for 72 hr, and the subculture tubes inoculated with the other test species were incubated at 30 C for 72 hr. Tubes were then examined for the presence or absence of growth of the test species.

Bactericidal Activity of Products in Aquaria Holding Fish

The ability of the products to reduce the viable aerobic bacterial count in aquaria water in the presence of goldfish (*Carassius auratus*) and guppies (*Lebistes reticulatus*) was tested at one, two, and four times the concentration recommended by the manufacturers. The fish were acclimatized in a holding aquarium for a minimum of 7 days before the assays. The bioassays were performed in 4-liter round glass jars, each containing 2 liters of well water. This well water supply has been used at this laboratory for 3 years to maintain a large fish population. The jars were aerated at 1 liter per min and held at 20 C. Six goldfish (mean weight 1.8 g) were placed in each of four assay jars, and twelve guppies (mean weight 0.4 g) were placed in each of four assay jars. The fish were held for 24 hr before the addition of the test formulation and were not fed until the end of the bioassay. The formulation under test was then added at the appropriate concentration to each of three jars containing goldfish and to each of three jars containing guppies. The other two jars were maintained as controls. Each jar was sampled immediately before addition of the product (zero time), as well as 30 min, 24 hr, and 48 hr after addition of the product. The bacterial load present in these water samples was determined by the drop pipet method of Miles and Misra (1938). The count procedure employed Standard Methods agar (BBL) plates and duplicate serial dilutions in sterile buffered distilled water. The plates were incubated at 20 C for 72 hr, and the colonies were then counted. At the end of the 48-hr bioassay, the fish were transferred to a second holding aquarium and observed for a further 7 days.

Results

When tested using the specifications recommended by the manufacturers (i.e. dilution, time of exposure, and temperature) the products did not inhibit the growth of any test species. The dilution of product able to inhibit growth of test species was markedly different from the dilution recommended (Table 1). Five products were bacteriostatic for all test species at the following dilutions: product 1 at 1:20; product 3 at 1:100; product 4 at 1:4; product 7 at 1:40; and product 11 at 1:2. The other formulations did not inhibit growth of all test species, even when used at a dilution of 1:2. In contrast, phenol diluted 1:200 (w/v) was bacteriostatic for all test species.

The products were not bactericidal or sporicidal at the dilutions, time of exposure, and temperature recommended for their use. Even though all products were tested at higher than recommended concentrations, only three formulations were bactericidal for all test species (Table 2). Product 7 diluted 1:2 was bactericidal for all test species at 30 min, and undiluted aliquots of products 1 and 13 were bactericidal for all test species at 60 min. Product 11 diluted 1:16 killed spores of *B. subtilis* at 10 min, but the other products were not sporicidal even when spores were exposed to undiluted aliquots for 60 min. In contrast, phenol diluted 1:70 (w/v) was bactericidal to all test species at 10 min (Table 2) and was sporicidal at 10 min when diluted 1:20 (w/v).

Table 3 shows that the number of viable bacteria in the water was not significantly reduced even when Products 2, 3, 6, 8, 10, 11, or 14 were added at four times the recommended concentration. Furthermore, within 90 min of the exposure to product 3 at dilutions of 1:2500 (four times recommended dilution) and 1:5000, the fish had turned on their sides and displayed little gill movement. All fish exposed to these concentrations were dead within 48 hr. Only two of the products (7 and 13) produced a significant reduction in the viable bacterial count when used at higher concentrations. Product 4 was also toxic to fish. Exposure of fish to a dilution of 1:4000 caused the death of all assay fish within 90 min. Because of this rapid death, bacterial counts were not performed.

Discussion

It is apparent that the products tested in this study would prove inadequate for the therapy and prophylaxis of bacterial infections of fish. Even in the absence of significant amounts of organic material, the products were unable to reduce the modest viable bacterial counts in the bioassay aquaria water. Concentrations of the products that were bacteriostatic or bactericidal were markedly higher than the recommended concentrations. These concentrations were likely to be toxic for fish. It should be noted that with product 13 in assays with *A. salmonicida*, *P. aeruginosa*, and *P. putida* the bactericidal concentration was less than the bacteriostatic concentration. This result is due to differences in the assay procedures. The organic material present in the bacteriostatic assay broths was sufficient to combine with and reduce the available concentration of $KMnO_4$ in these assays, whereas the bac-

TABLE 2. Bactericidal activity of aquarium aids.

Test organism	Time of exposure (*min*)	Product tested											
		1	2	3	4	6	7	9	10	11	13	14	Phenol
A.		1:4[a]	Undil	Undil	Undil	1:2	1:10	Undil	Undil	1:28	1:4	Undil	1:135
liquefaciens	5	+[b]	+	+	+	+	+	+	+	+	+	+	+
14715	10	0[c]	+	+	+	0	0	+	+	0	+	0	0
	15	0	+	0	+	0	0	0	+	0	+	0	0
	30	0	+	0	+	0	0	0	0	0	+	0	0
	60	0	+	0	0	0	0	0	0	0	0	0	0
A.		1:6	Undil	1:50	1:2	1:2	1:22	1:2	1:2	1:40	1:4	1:4	1:150
salmonicida	5	+	+	+	+	+	+	+	+	+	+	+	+
14174	10	0	+	0	+	0	0	+	0	0	0	0	0
	15	0	+	0	+	0	0	0	0	0	0	0	0
	30	0	0	0	0	0	0	0	0	0	0	0	0
	60	0	0	0	0	0	0	0	0	0	0	0	0
C.		Undil	Undil	1:2	Undil	Undil	1:6	Undil	Undil	1:50	Undil	Undil	1:70
columnaris	5	+	+	+	+	+	+	+	+	+	+	+	+
23463	10	+	+	0	+	+	0	+	+	0	0	+	0
	15	+	+	0	+	+	0	+	+	0	0	+	0
	30	0	0	0	+	+	0	+	+	0	0	+	0
	60	0	0	0	+	+	0	0	+	0	0	+	0
M.		1:2	Undil	1:45	Undil	1:2	1:8	1:2	Undil	Undil	1:2	Undil	1:75
marinum	5	+	+	+	+	+	+	+	+	+	+	+	+
927	10	+	+	0	+	0	0	0	+	+	0	+	0
	15	+	+	0	+	0	0	0	+	+	0	+	0
	30	0	+	0	+	0	0	0	+	+	0	+	0
	60	0	+	0	+	0	0	0	+	+	0	+	0
P.		Undil	Undil	1:42	Undil	Undil	1:2	Undil	Undil	1:6	1:4	Undil	1:95
aeruginosa	5	+	+	+	+	+	+	+	+	+	+	+	+
15442	10	+	+	0	+	0	+	+	+	0	+	+	0
	15	+	+	0	+	0	+	+	+	0	+	+	0
	30	0	+	0	+	0	0	+	+	0	+	+	0
	60	0	+	0	0	0	0	+	+	0	0	+	0
P.		Undil	Undil	Undil	Undil	1:6	1:10	Undil	Undil	1:14	1:4	Undil	1:125
putida	5	+	+	+	+	+	+	+	+	+	+	+	+
12633	10	+	+	+	+	0	0	0	0	0	+	+	0
	15	0	+	+	+	0	0	0	0	0	+	+	0
	30	0	+	+	0	0	0	0	0	0	+	+	0
	60	0	0	+	0	0	0	0	0	0	0	+	0
S.		Undil	Undil	1:25	Undil	Undil	1:2	Undil	Undil	1:6	1:4	Undil	1:90
aureus	5	+	+	+	+	+	+	+	+	+	+	+	+
6538	10	+	+	0	+	0	0	+	+	0	0	+	0
	15	+	+	0	+	0	0	+	+	0	0	+	0
	30	+	+	0	+	0	0	+	+	0	0	+	0
	60	0	+	0	+	0	0	+	+	0	0	+	0

[a] Dilution (v/v) of product tested (not based on active ingredients).
[b] + is growth after exposure to product.
[c] 0 is absence of growth after exposure to product.

tericidal assays were performed in water and the $KMnO_4$ was not inactivated. This was also true for bacteriostatic and bactericidal assays of the Ag_2O in product 14 with *A. salmonicida* and the malachite green in product 11 with *P. aeruginosa.*

TABLE 3. Effect of aquarium aids on viable bacterial numbers in water containing goldfish or guppies.

Product tested	Estimated numbers of bacteria in aquarium water (× 10^5/ml) after addition of test product			
	0 min[a]	30 min	24 hr	48 hr
Product 2	Guppies			
1:2500[b]	18	10	88	52
Nil[c]	13	16	84	11
Product 3	Goldfish			
1:2500	9	7	10	19
1:5000	7	7	12	19
1:10,000	7	9	14	30
Nil	11	12	10	8
Product 6	Guppies			
1:275	20	11	89	39
Nil	13	16	84	11
Product 7	Guppies			
1:500	10	3	0.1	9
1:1000	10	8	0.2	33
1:2000	10	8	35	14
Nil	10	11	10	11
Product 8	Goldfish			
1:225	10	13	28	36
1:450	9	12	44	18
1:900	9	13	25	22
Nil	16	22	26	34
Product 10	Goldfish			
1:500	4	3	48	60
1:1000	2	1	9	7
1:2000	3	2	9	5
Nil	3	3	1	1
Product 11	Goldfish			
1:22,500	50	52	240	156
1:45,000	95	50	120	226
1:90,000	62	95	320	953
Nil	25	20	230	212
Product 13	Guppies			
1:450	4	0.005	0.005	0.3
1:900	10	0.02	0.5	3
1:1800	3	0.2	1.5	5
Nil	4	2	4	9
Product 14	Guppies			
1:3750	21	18	31	13
1:15,000	17	19	24	36
Nil	13	16	84	11

[a] Before addition of product.

[b] Final dilution (v/v) of product in aquarium water (not based on active ingredients).

[c] Control aquarium.

It should also be noted that the bacterial numbers in the control aquaria did not increase significantly over the 48 hr bioassay period. This likely reflects the near maximum population of "free" bacteria available in the aquaria water under the conditions of the bioassay, and probably represents a balance between the numbers of "free" organisms in the water and those present on the aquaria surfaces. Because of this, the bioassay techniques used in this study only allowed the bactericidal activity of the products to be evaluated.

The most convenient method of use of these formulations, and that recommended by the manufacturers, is the addition of the formulation to the aquarium water. There is little evidence however that this method has proved effective for systemic infections of fish. Treatment of such infections generally requires that the antibacterial compound be administered orally or parenterally (Herman 1970). Addition of antibacterials to the water is likely only to limit the growth of the bacterial flora in the aquarium, and may reduce the bacterial numbers in lesions on the surface of the fish. Control of this bacterial growth in the water by the addition of the antibacterials to the water may further be complicated by the presence of sand, plants, and food; since these will reduce the efficiency of the disinfection either because of direct inactivation of the antibacterial or through protection of the bacteria from attack (Sykes 1967).

It is also desirable that formulations designed to lower the bacterial numbers in aquarium water are active against human pathogens since a wide variety of bacterial species able to cause diseases of man are able to grow using fish foods as sole source of nutrients (Trust and Money 1972). Because of the potential ability of these bacteria to multiply in an aquarium, the aquarium may present a public health risk by transfer of the organisms to people. Such transfer leading to salmonellosis has been shown from aquaria housing tortoises (Boycott et al. 1953) and from pet turtles (Bowmer 1971). Furthermore, the United States Center for Disease Control recently estimated that some 300,000 cases of salmonellosis are associated each year with such infected turtles (Bowmer 1971). Skin lesions due to aquarium-borne mycobacteria have also been reported (Adams et al. 1970, Månsson et al. 1970).

Since aquarium fishes are used in a number of areas of research, it is important that workers be aware of the limitations of these commercial formulations. Also, the use of products containing low levels of sulfa drugs is to be discouraged since, apart from being ineffective, they may encourage the development of sulfa-drug-resistant strains of bacteria. Furthermore, the results of this study suggest that many of the materials commonly employed in other areas of fish culture may be inadequate and need to be re-evaluated. Such evaluations are important since, although other studies have shown that there is no perfect antiseptic (Sykes 1967), adequate antiseptics are desirable because the prevention of infections on the body surface and the killing of bacteria in the environment is better performed by antiseptics than by antibiotics (Hughes and Stewart 1971). The selection of suitable antiseptic agents for various purposes, coupled with the use of sterile foods, would contribute substantially to the control of fish disease.

Acknowledgments

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Migration of Yearling Sockeye Salmon (*Oncorhynchus nerka*) as Determined by Time-Lapse Photography of Sonar Observations

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Groot, C. 1972. Migration of yearling sockeye salmon (*Oncorhynchus nerka*) as determined by time-lapse photography of sonar observations. J. Fish. Res. Bd. Canada 29: 1431–1444.

The seaward migration of sockeye salmon smolts through the Babine Lake system to its outlet was examined by taking film records of the Plan-Position-Indicator display of a high-frequency sonar whereby each frame of film was exposed during one scan of the sonar unit. Frame-by-frame analysis of the films revealed information on speed, direction, and diurnal timing of migration of sockeye smolts during a 24-hr period.

Migratory activity in the lake centered around dusk and dawn, a similar pattern to that near the outlet for smolts entering the river on their way to sea.

Speeds of movements were 19–51 cm/sec (mean 30 cm/sec). Greatest velocities occurred at dusk and dawn. They were close to the maximum sustained swimming speeds determined under laboratory conditions for sockeye smolts of the same size and within similar temperature ranges as in the field.

The most direct movements of targets were found at twilight, when migration activity was highest. In general, directional tendencies were consistent with the shortest route to the outlet. In some observations near the junction of Main Lake and Morrison and North arms, movements were observed which would lead the smolts away from the outlet. Consequences of such movements are discussed and compared with data from tagging operations.

Groot, C. 1972. Migration of yearling sockeye salmon (*Oncorhynchus nerka*) as determined by time-lapse photography of sonar observations. J. Fish. Res. Bd. Canada 29: 1431–1444.

L'auteur a étudié, dans le système du lac Babine jusqu'à sa sortie, la migration vers la mer de smolts de saumon sockeye. Dans ce but, il a photographié l'image sur l'écran d'un sonar à haute fréquence, au rythme d'une image par tour de balayage du sonar. L'examen, image par image, des films a fourni des renseignements sur la vitesse, la direction et l'horaire de la migration sur une période de 24 heures.

Dans le lac, l'activité migratoire est concentrée surtout au crépuscule et à l'aube. Il en est de même, près de la sortie, pour les smolts qui pénètrent dans la rivière en route vers la mer. La vitesse des déplacements varie de 19 à 51 cm/sec (moyenne de 30 cm/sec). Les vitesses sont maximales au crépuscule et à l'aube. Elles se rapprochent des vitesses maximales soutenues observées au laboratoire avec des saumons sockeye de même taille et à une même gamme de températures que sur le terrain. Les mouvements les plus directs des poissons cibles se produisent au demi-jour, alors que l'activité migratoire est à son maximum. La résultante directionnelle des déplacements correspond généralement à la route la plus courte vers la sortie du lac. Il est arrivé toutefois qu'au cours d'observations au confluent du lac Main et des bras Morrison et Nord, l'auteur ait noté des déplacements qui auraient éloigné les smolts de la sortie. Il discute des conséquences de tels déplacements et les compare avec les résultats de marquages.

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Sockeye salmon (*Oncorhynchus nerka*) generally spawn in creeks and rivers adjacent to lakes. In the Babine Lake system in north–central British Columbia, breeding grounds are separated in three areas. After entering the lake, the juveniles from these areas remain segregated in three groups (Johnson and Groot 1963), the Nilkitkwa Lake and North Arm, the Morrison Arm, and the Main Lake demes (deme is here used for a reproductively more-or-less isolated group of a population) (Fig. 1). This distribution is consistent during the year of freshwater life, up to the time of seaward migration of yearling sockeye, known at this stage of their life as smolts.

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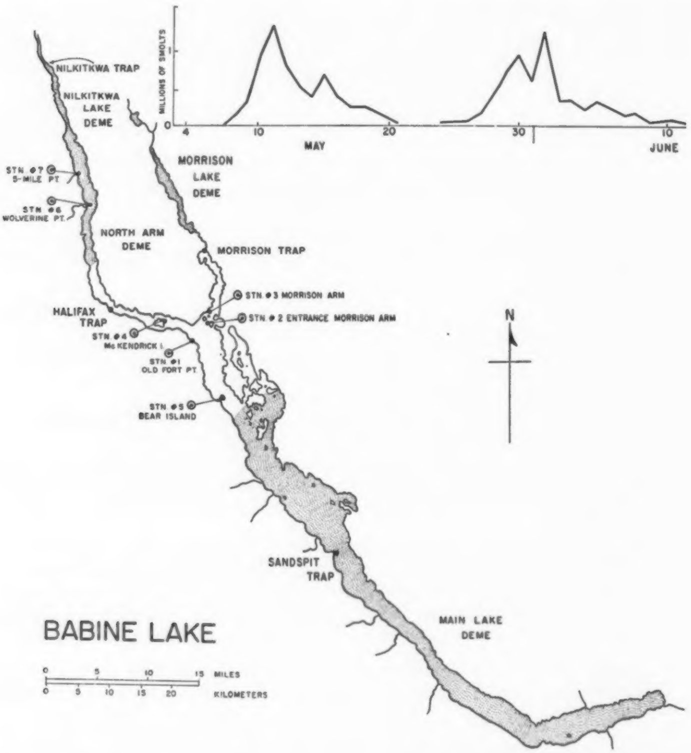
MILLIONS OF SMOLTS
0
1
4
10
20
30
10
MAY
JUNE
NILKITKWA TRAP
NILKITKWA LAKE DEME
MORRISON LAKE DEME
STN #7 5-MILE PT.
STN #6 WOLVERINE PT.
NORTH ARM DEME
MORRISON TRAP
STN #3 MORRISON ARM
STN #2 ENTRANCE MORRISON ARM
HALIFAX TRAP
STN #4 Mc KENDRICK I.
STN #1 OLD FORT PT.
STN #5 BEAR ISLAND
N
SANDSPIT TRAP
MAIN LAKE DEME
BABINE LAKE
0 5 10 15 MILES
0 5 10 15 20 KILOMETERS

FIG. 1. Map of the Babine Lake system showing the distribution of the three demes of sockeye smolts prior to migration and the location of the seven stations where sonar films were taken. The line connecting center with circumference at each station indicates the midpoint direction of scanning. The graph illustrates the estimated smolt migration at the outlet in 1963.

The seasonal time pattern of sockeye smolt migration in Babine Lake, as assessed from trapping part of the run at the outlet, shows two peaks (Fig. 1). Such a bimodal frequency distribution of daily catches can be expected when migration from all points of the lake commences at about the same time (Johnson and Groot 1963). First, smolts close to the outlet in Nilkitkwa Lake and the North Arm move out, giving rise to the first mode. Following, smolts from the Main Lake area and Morrison Lake reach the outlet, resulting in the second mode.

The main process of smolt migration can only be directly observed during dusk and dawn hours under calm weather conditions, when smolts come close to the surface. New techniques developed for the detection of fish, especially that of echo-sounding and ranging, have recently made it possible to study movements of fishes under natural conditions (Tucker 1967; Harden Jones 1968). The purpose of this paper is to discuss observations of sockeye smolt migration from the nursery areas to the outlet made by a combination of a high-frequency sonar and time-lapse photography. This technique for following migrating sockeye salmon in Babine Lake at all times of the day and at different depths was developed by Groot and Wiley (1965) to obtain detailed information on speed, direction, and intensity of movement on a continuous basis.

Materials and Methods

The sonar and time-lapse photography technique used in this study has been described in detail by Groot and Wiley (1965). Observations were made with a Honeywell sea scanner Model 1B (132 KHz), which scans an area of 180° over ranges of 124, 248, and 496 m. Targets detected during each scan and displayed on a Plan-Position-

Indicator (PPI) scope were photographed on one frame of cine film. Echo-signals of moving targets recorded during subsequent scans appear slightly displaced on following frames in a pattern related to the actual movement of the target. Since one 180° scan lasts 11.3 sec at the 124 m and 22.6 sec at the 248 m range, movements on the film are speeded up about 270 and 540 times, respectively, when the film is projected at 24 frames per sec. This allows one to view movements of fish during a 24-hr period in 5 or 2.5 min, depending on the range used, 124 or 248 m. Because of the compression of time on the film records, moving targets are easily separated from stationary ones.

It is essential that the gear is in a fixed position so that the same area is scanned each time (Fig. 2). The barge housing the sonar and photographic equipment was therefore anchored to shore in sufficiently deep water. In general, scanning sessions were carried out over 24 hr to obtain information on diel patterns of migration parameters.

The greatest problem in the interpretation of echo-signal displays is that of target identification. Arguments for considering the moving targets displayed on the PPI-scope as representing sockeye smolt schools have been given by Groot and Wiley (1965). These arguments were derived from (i) simultaneous comparison of echo-signal display with near surface migratory activity, (ii) close correlation of diel timing of moving targets with migration intensity at the outlet of the lake, and (iii) similarity in average velocity of movement between moving targets and sockeye smolts migrating near the surface. Extensive purse seine operations have further shown that sockeye salmon constitute the major proportion of fishes (up to 97%) in Babine Lake during early spring (Scarsbrook and McDonald MS 1970).

Films of sonar observations were made at seven locations in Babine Lake, May 20–June 22, 1963 (Fig. 1). All film records were analyzed frame-by-frame with a time–motion projector. Examples of moving targets at different times of the day plotted on a grid similar to that on the PPI-scope are shown in Fig. 3. Targets appearing on less than four frames in succession were not used in the analysis, since it is doubtful if these indicate echoes from fish.

If the tracks of the moving targets are relatively straight, the general direction of movement can easily be determined and plotted in a circular scatter diagram (Fig. 3A). This is more difficult in cases of irregular movement patterns as, for example, during the early morning periods (Fig. 3B, 0445–0500 hr). Therefore, in most of the following figures, two directions of movement are presented for each moving target; namely, the direction of the first six (in-movement) and the last six (out-movement) echo-signals (Fig. 5A). Comparison of these two directions gives an indication of how direct movements of targets are at different times of the day. All compass directions are given in degrees true North.

Mean direction (α) and mean vector length ($\bar{a}$) were determined by vector addition. The modified Rayleigh test (Batschelet 1965) was used to indicate departure from uniformity. Differences from uniformity are indicated by the pattern of the triangle at the outside of the scatter diagrams: all black $P<0.01$, half black-half white $0.05>P>0.01$, and all white $P>0.05$ (Fig. 5).

Sometimes migration directions in different or in 180° opposite directions occurred (for examples see Fig. 6C 0400–0715 hr; Fig. 7A 2000–2230 hr). These give rise to bimodal vector distributions which are difficult to analyze with available techniques. Where bimodality is clearly indicated, the mean direction of the modes is calculated separately by adding the vectors over three 45° classes around each mode (Fig. 6C and 7A). Dotted symbols are used in these cases and no statistical significance is indicated since the distribution of data points

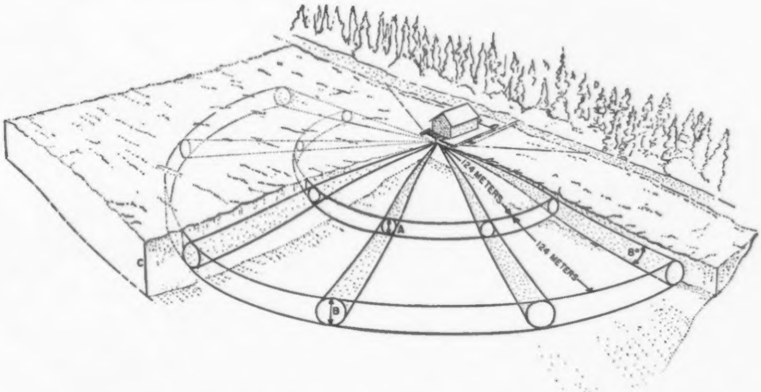

FIG. 2. Diagram of scanning arrangement with sonar barge anchored to shore. Beam width of cone is 8° (± 1°) at the –3db level and side-lobe radiation is suppressed to –20db level or lower. A, diameter of sound beam at 124 m is about 18 m and B, at 248 m about 36 m. C, depth of water, which had to be at least 5 m under sound dome and more than 30 m at a range of 124 m.

contained in each mode is obscured. In addition, mean direction and mean vector length of the total vector distribution are also presented, although the biological value of these data points are doubtful.

Diagrams as illustrated in Fig. 3 also give information on speed of moving targets, since total distance can be measured from length of track in relation to scanning range, and duration of track is known from the number of frames of film the target could be followed (time lapse between frames was approximately 11.3 and 22.6 sec for ranges of 124 and 248 m, respectively).

Diurnal timing of movement intensity was examined by counting the number of moving targets per 15-min analysis period. There are, however, some problems in

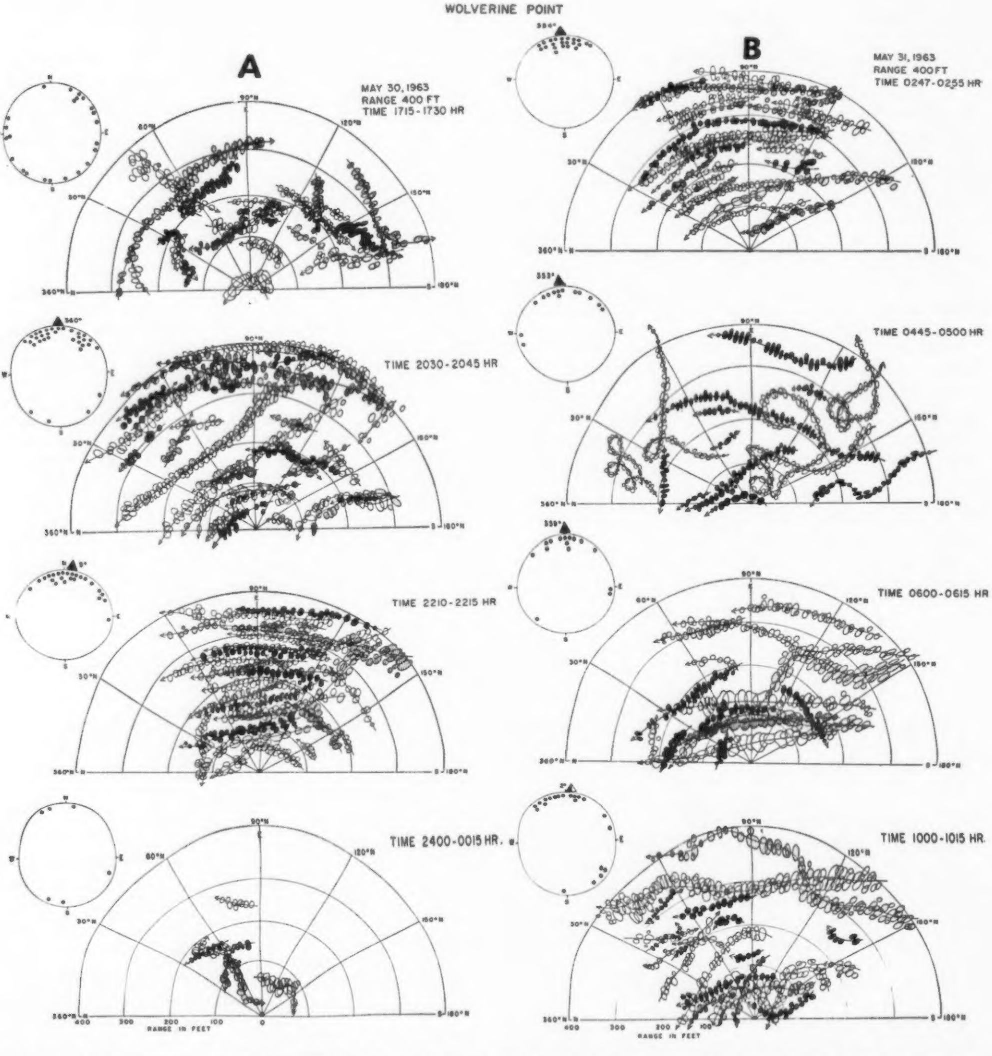

FIG. 3. Movements of targets at different times of the day obtained from a frame-by-frame analysis of a sonar film taken at Wolverine Point, May 30–31, 1963. A, time periods 1715 till 0015 hr PST. and B, 0247 till 1015 hr PST. Scatter diagrams illustrate directions of movement (one dot for direction of first part of each track) and mean directional tendency (▲) in degrees north.

translating these values into migration intensity. The main difficulty is that school size is not constant over a 24-hr period, or during the same time period on different days. Visual and echo-sounding observations during the dusk period indicate that schools break up with increasing darkness and regroup again after dawn (Narver 1970). On some sonar film records, this process is clearly shown by changes in size of targets with time of day (Fig. 3). All times are Pacific Standard.

Another difficulty is that numbers of moving targets between observation stations cannot be compared with each other. Migration from the Main Lake into the North Arm proceeds from a big body of water into a relatively narrow arm and this obviously results in an increase in number of targets per volume of water. Comparison of movement intensity per time unit can thus be made only between observations at each station and not between stations.

Results and Discussion

DIURNAL TIMING OF MOVEMENT

The number of detected targets that are moving per 15 min shows in general a bimodal distribution with modes near dusk and dawn (Fig. 4). A number of sources give evidence that this is the general migratory activity rhythm of smolts during seaward migration from the nursery areas in lakes to the outlet (Johnson and Groot 1963; Groot 1965). For example, the exodus of smolts from lakes, as determined by catches at the outlet, characteristically shows peaks at dusk and dawn with the dusk peak often being the greater. Further, two activities indicative of migration observed in aquaria-held smolts show diurnal peaks at dusk and dawn,

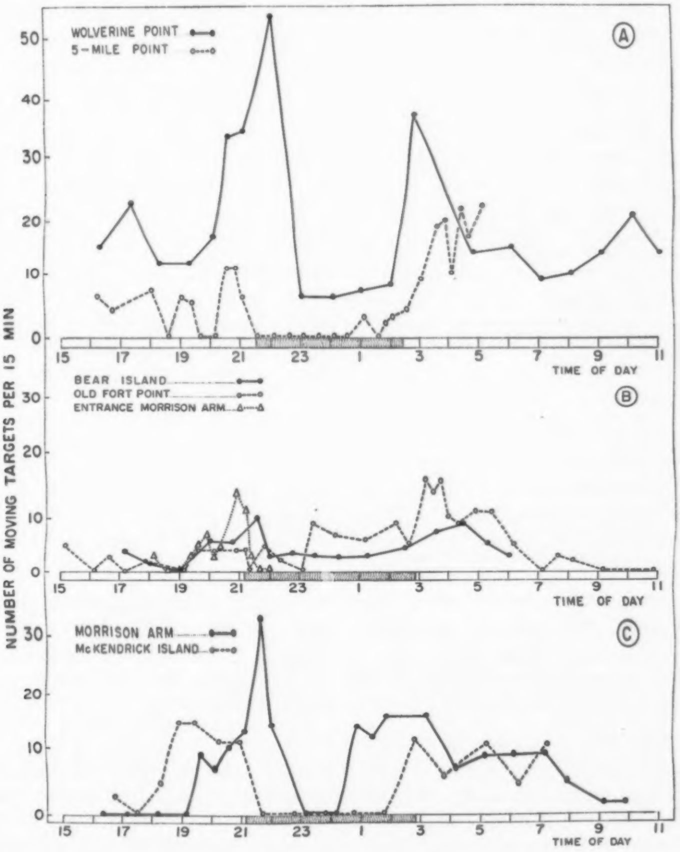

FIG. 4. Diel distribution of moving targets per 15-min period at different observation locations.

strongly suggesting that the diel timing of migration primarily falls during twilight periods.

As mentioned before, number of moving targets cannot be translated directly into number of moving fish, since the number of fish per target changes with time of day. Especially at night, schools seem to break up, resulting in many small targets on the PPI-scope. However, these small targets do not move appreciably or cannot be followed for four or more frames of film and thus are not included in the analysis. Target size grows soon after dawn and it is difficult to determine how to compare these big early morning echo-signals with the smaller ones during the twilight periods. There is, however, a marked difference in the directiveness of movements during the dusk–dawn and early morning periods. This is clearly indicated by viewing the films at 24 frames per sec and is also shown in the diagrams in Fig. 3. Note how the movements during the period 2210–2215 hr and 0247–0255 hr all have rather direct courses, while movements at other times of the day are more irregular, especially during the early morning hours (Fig. 3B, 0445–0500 hr). Despite the problem of equating number of moving targets to number of fish, one can conclude that migration in the lake also occurs primarily around dusk and dawn, similar to that at the outlet. There are exceptions to this general conclusion; the Old Fort Point data show little movement during dusk and increasing activity during the night with a peak around dawn (Fig. 4B). This may indicate that we are dealing with a more complicated situation in this area (see below).

SPEED OF MOVEMENT

Target speeds can be determined, since both length of tracks and times to cover them are known. These speeds are the resultants of actual swimming velocities and water movements. Currents were not measured during the 1963 sonar observations. However, current measurements during 1961 and 1962 in the North Arm and near Old Fort indicated that there is no simple flow pattern of water into and through the North Arm towards the outlet; currents near the surface, where most of the migration activity occurs, are primarily dependent on wind direction (Johnson and Groot 1963 and unpublished data).

Sonar observations were made only during days with little or no wind, since it was difficult to keep the sonar barge firmly secured in winds of more than 15 km/hr. The effects of wind-driven currents are considered of little importance in the present observations; consequently the speeds calculated from the film analysis should be close to actual swimming speeds.

Table 1 shows an increase in target velocity from about 22–33 cm/sec during the day and night to about 41–51 cm/sec during dusk and dawn for the Wolverine Point observations. At Five Mile Point a maximum target speed of 48 cm/sec occurs during dusk. Cruising speeds of sockeye salmon juveniles determined experimentally by Brett (1965) show that smolts of the size (about 8 cm) and in the temperature range (10–15 C) we are dealing with are capable of maximum sustained swimming speeds of about five to six lengths per sec (40–50 cm/sec). This suggests that sockeye smolts during the twilight observation periods in the North Arm swam close to their maximum continuous performance capability.

The slower speeds at other times of the day for the Wolverine and Five Mile point observations can be interpreted in two ways: either the fish schools were moving slower at these times or the movements were less directed both in the horizontal and vertical planes as compared with the dusk and dawn periods. The transducer of the Honeywell sea scanner radiates an 8° (±1°) conical beam (Fig. 2). Thus, at a distance of 124 m the scanning field depth is about 18 m, which is sufficient to record schools swimming up or down at 30° from the horizontal for 87 sec (7–8 scans or frames) when moving at 40 cm/sec. Sockeye schools travelling at constant depth will stay longer in the scanning area and produce longer tracks. Wolverine Point tracks were shortest at night (2400–0015 hr) and this is true for most of the other locations (Table 2). Longest tracks occurred during early morning at Wolverine Point; the swimming speed at this time (27 cm/sec) is approximately half of that during dawn (51 cm/sec). This leads to the conclusion that sockeye smolts at Wolverine Point were swimming faster during dusk and dawn compared with other times of the day, and that at night movements diverted most from horizontal as indicated by the short tracks on the scope. Observations at other places in Babine Lake in 1963 did not indicate such marked changes in swimming speed at different times of the day (Table 1) nor do they suggest any consistent diel patterns in distances of track (Table 2). In these cases, sockeye smolts moved on the average at velocities 25–41 cm/sec during twilight periods which is from half to about maximum sustainable swimming velocity found under laboratory conditions.

From tagging and recovery operations in Babine Lake, Johnson and Groot (1963) calculated that average rates of travel of sockeye smolts from nursery areas to outlet ranged from 5.1 km/day in 1960 to 7.8 km/day in 1961. Direct measurements of swimming speeds of near-surface, migrating schools during these two years showed speeds between 20 and 30 cm/sec with a mean of 24.5 cm/sec. This suggests that sockeye smolts swam between

TABLE 1. Average speeds in centimeters per second of sockeye smolt movement and number of measurements in parentheses at seven locations in Babine Lake at different time periods of the day.

Location: Range:	Wolverine Pt. *124m*	Five Mile Pt. *248 m*	Bear Is. *248 m*	Entrance Morrison Arm *124 m*	Old Fort Pt. *248 m*	Morrison Arm *124 m*	McKendrick Is. *248 m*	Mean
1630–1930	22.6(47)	30.8(22)	22.6(11)	20.7(9)	40.8(5)	–	33.2(74)	29.9(168)
1930–2230 (dusk)	41.1(122)	47.9(28)	24.4(49)	27.7(48)	29.6(23)	36.0(86)	36.0(43)	35.7(399)
2230–0130 (night)	22.3(14)	28.3(2)	18.9(25)	–	25.3(22)	25.3(26)	–	22.6(89)
0130–0430 (dawn)	51.2(36)	28.0(90)	27.1(42)	–	30.8(79)	25.9(39)	36.6(35)	30.8(321)
0430–0730	26.8(37)	25.6(37)	26.8(17)	–	22.6(27)	40.5(27)	27.4(52)	27.1(197)
0730–1030	27.4(38)	–	–	–	30.5(5)	33.2(9)	–	28.7(52)
1030–1330	33.2(10)	–	–	–	28.3(18)	–	–	29.3(28)
1330–1630	22.9(12)	28.0(6)	–	–	20.1(12)	–	–	23.8(30)
Mean	33.5(316)	30.2(185)	24.4(144)	26.2(57)	27.4(191)	32.9(187)	32.6(204)	30.3(1284)

TABLE 2. Average length in meters of tracks of sockeye smolt and number of measurements in parenthesis at seven locations in Babine Lake at different time periods of the day. Note that sonar range varies from 124 to 248 m.

Location:	Wolverine Pt.	Five Mile Pt.	Bear Is.	Entrance Morrison Arm	Old Fort Pt.	Morrison Arm	McKendrick Is.
Range:	*124 m*	*248 m*	*248 m*	*124 m*	*248 m*	*124 m*	*248 m*
1630–1930	40.5(47)	79.4(22)	56.2(11)	27.1(9)	64.5(5)	–	105.2(74)
1930–2230 (dusk)	68.2(122)	110.0(28)	56.6(49)	30.1(48)	39.0(23)	46.0(86)	87.8(43)
2230–0130 (night)	26.3(14)	64.0(2)	47.6(25)	–	43.6(22)	30.7(26)	–
0130–0430 (dawn)	60.8(36)	74.3(90)	56.9(42)	–	58.8(79)	35.2(39)	80.3(35)
0430–0730	72.9(37)	84.6(37)	86.2(17)	–	71.3(27)	54.5(27)	82.3(52)
0730–1030	46.1(38)	–	–	–	82.8(5)	43.8(9)	–
1030–1330	29.9(10)	–	–	–	78.2(18)	–	–
1330–1630	31.5(12)	162.3(6)	–	–	64.6(12)	–	–

6½ hr (1960) and 8½ hr (1961) each day on a direct course.

Film analysis of the 1963 sonar observations indicates a swimming speed range 19–51 cm/sec with a mean of 30 cm/sec (Table 1). This is faster than the near-surface migrating speed. To cover daily distances of 5.1 and 7.8 km the smolts would have had to swim on direct courses between 3.2 and 5.5 hr in 1960 and between 4.8 and 8.4 hr in 1961. Although a number of sources (see Johnson and Groot 1963; Groot 1965) indicate that approximately this number of hours each day is spent in active migration, Fig. 4 shows that movements in the lake are often evident during many hours in addition to the twilight periods. However, in the next section it is shown that movements during day and night are generally not directed towards the outlet.

DIRECTION OF MOVEMENT

Sonar observations of sockeye smolt migration in the North Arm were made at Wolverine and Five Mile points (Fig. 1). Examples of directions of movement at Wolverine Point during different times of the day are presented in Fig. 2 and these, together with the Five Mile findings, are summarized in Fig. 5. The total observation period is divided in 3- to 4-hr intervals and frequency distributions over a number of 15-min periods within each interval are accumulated.

Movements were well directed during dusk, dawn, and early morning periods. These periods also show greatest consistency between in- and out-directions, indicating that schools moved over rather direct courses. During late afternoon and midnight periods, the distribution of directions is not significantly different from uniformity at the 5% level. Late morning movements at Wolverine Point show more spread in directions and indicate less direct tracks compared with dusk, dawn, and early morning (Fig. 3B and 5A). A significant preferred direction is still apparent for movements during this period, however.

During times of most direct movements (dusk and dawn), mean directional choices range 311°N–4°N, or between NW and N (Fig. 5). The direction along the North Arm and Nilkitkwa Lake towards the outlet is about 350°N (Fig. 1). Directions of migration of sockeye smolts near Wolverine and Five Mile points are thus appropriate for reaching the outlet by the shortest route.

Before their migration starts, sockeye smolts in the Babine Lake system are separated in three demes (Fig. 1). The question therefore arises, from which deme or demes did the smolts passing Wolverine and Five Mile points on the observation days originate? According to Johnson and Groot (1963), smolts from all parts of the lake seem to commence migration towards the outlet during the first week of May. In 1963, most of the smolts from the Nilkitkwa and North Arm deme had left the lake by about May 20 (Fig. 1, first mode of insert). The Wolverine Point sonar observations were made on May 30–31, when migration of Main and Morrison lake demes started to peak at the outlet (Fig. 1, second mode of insert), while the Five Mile Point observations on June 21–22 coincide with the tail end of migration from these two demes.

The outlet is 34 and 24 km away from Wolverine and Five Mile points, respectively, and since smolts in the North Arm travel about 8–10 km per day (Johnson and Groot 1963), the remaining distance to the Lower Babine River can be covered in 3–4 days. It therefore seems obvious that the sockeye

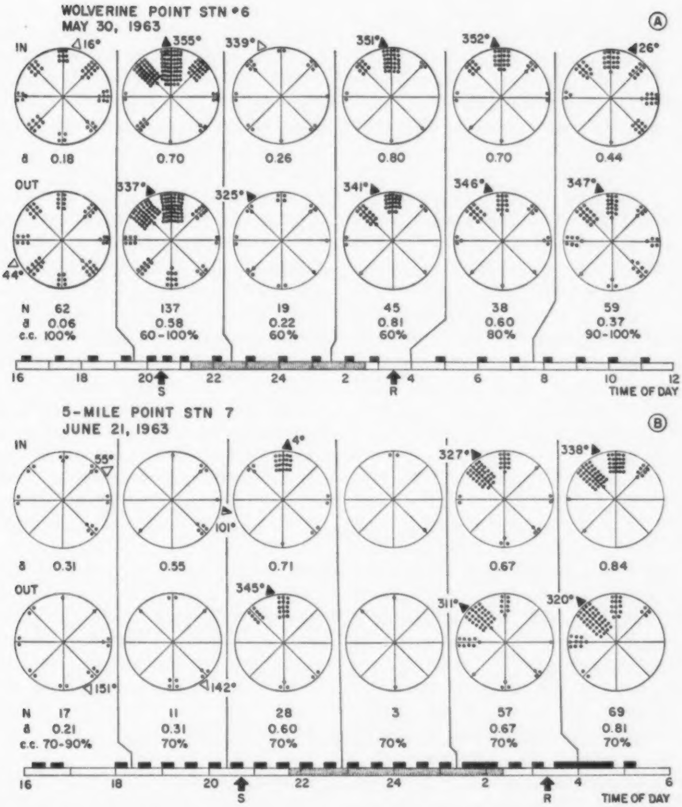

FIG. 5. Distributions of directions of targets from analysis of first six (in-movement) and last six (out-movement) frames of film recording of each track at Wolverine (A) and 5-Mile (B) points for different times of the day. One dot relates to one target. Triangles outside circular diagrams give mean direction in N°. Departure from uniformity is indicated by pattern of triangle (▲$P<0.01$, ▲$0.01<P<0.05$, △$P>0.05$); N, total number of targets per time period; $\bar{a}$, vector strength; cc, cloudcover in percentages from 0 to 100%. Black bars on time scale indicate sections of film analysed. S, sunset; R, sunrise. Dotted part of time scale illustrates night period from evening to morning civil twilight.

smolts observed near Wolverine and Five Mile points in the North Arm were of Morrison and Main lakes origin. No direct counts are available of the number of smolts these two demes contributed to the second mode at the outlet. Considering the escapement of adults to the spawning grounds in 1961, 23,600 to the Morrison Lake area and 321,400 to the Main Lake area (Smith MS 1967), the proportions of Morrison smolts in 1963 would have been about 7% of those leaving the Main Lake area when survival rates are equal for both demes. Thus, smolts observed at Wolverine and Five Mile points in 1963 must have been primarily of Main Lake origin.

Three sonar films were made in the Main Lake area; namely, at Bear Island, Old Fort Point, and the entrance of Morrison Arm (Fig. 1). Results from analyses of these films will be discussed next, starting with Bear Island.

OBSERVATIONS IN THE MAIN LAKE AREA

On May 28–29, recordings of smolt movements were made near Bear Island, looking across a deep channel between this island and the west shore of the lake. The sonar range was 248 m.

Only during late afternoon (1700–1930 hr) and dawn periods were the distributions of movements significantly different from uniformity (Fig. 6A). The mean directions for these two periods range 324°N–357°N. Comparison of in- and out-movements shows reasonable similarity, indicating that the fish travelled over rather direct courses.

The long axis of the Main Lake near Bear Island is about 320°N (Fig. 1) in the direction of the outlet. Thus, directions of movement during late afternoon and dawn periods correlate with the direction of the shortest route to the outlet. This is also the case for the dusk observations, although the distribution in this period is not significantly different from uniformity (Fig. 6A). Random directions are also found for night and late morning periods, but smolts usually do not migrate during these times.

Observations in the Main Lake area near the entrance of Morrison Arm (Fig. 1) made on May 21 show a mean direction of 342°N for the in- and 354°N for the out-movement during evening twilight (Fig. 6B). This is similar to directions found near Bear Island during times of migration (Fig. 6A). However, if smolts passing the entrance of Morrison Arm continue to travel NNW to N, they end up in Morrison Arm instead of the North Arm (see Fig. 1). There is evidence that this does happen; five smolts tagged during a tagging program at the Sandspit trap in 1962 were recovered in the Morrison trap (W. E. Johnson personal communication).

On May 20–21 sonar observations were made across from the entrance of Morrison Arm at Old Fort Point (Fig. 1) with a scanning range of 248 m. Figure 4B shows that smolts at Old Fort Point moved primarily during dawn and early morning hours, and only during these hours do movement

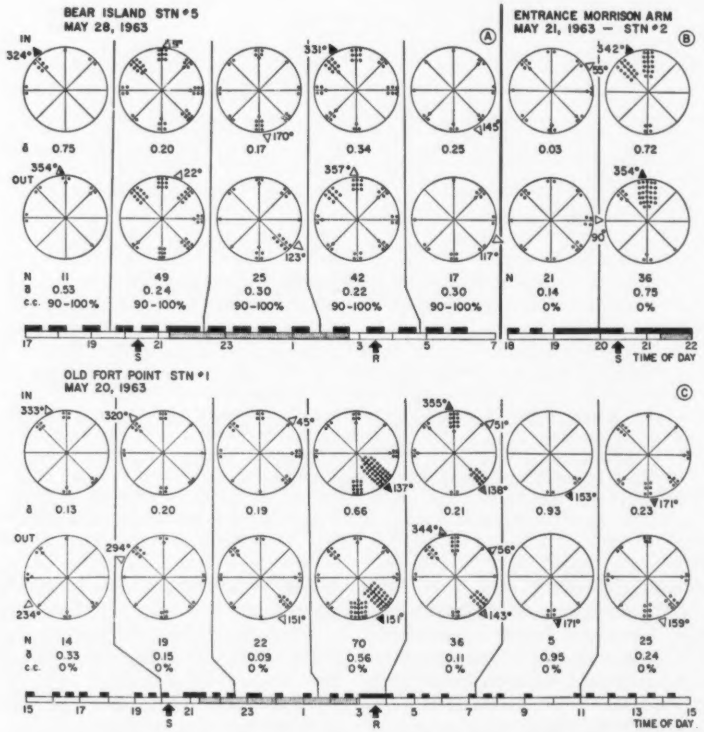

FIG. 6. Distributions of directions of moving targets at Bear Island (A), Entrance Morrison Arm (B), and Old Fort Point (C) for different times of the day. For further details see legend Fig. 5. Dotted triangles give mean directions for bimodal distributions. Direction of each mode has been determined separately and no departure from uniformity is indicated (see text for details).

distributions differ from uniformity (Fig. 6C). Directional tendencies during the 0400–0715 period strongly suggest two modes; one in a SE direction and another one in a NNW to N direction. The latter is appropriate for reaching the outlet. The SE mode, 138°N–143°N, corresponds with the mean directions, 137°N–171°N, indicated for the dawn and morning observations (Fig. 6C), which is opposite to the expected direction for Main Lake smolts. If these smolts continue on this course they will travel about 112 km before reaching the south end of the lake and will then be about 160 km from the outlet; the time required to cover these distances makes it doubtful whether they will get out of Babine Lake during the current season. Since very few smolts remain in the Main Lake area after the migration period (Scarsbrook and McDonald MS 1970), it is reasonable to conclude that we are dealing here with a temporary phenomenon of "reversed migration." Movements in opposite directions to those expected are commonly seen during visual observations of smolt migration in Babine Lake (Groot 1965).

Another possible explanation for the reversed directions is that smolts migrating out of Morrison Arm, after crossing the Main Lake to Old Fort Point, turn SE on reaching the shore (Fig. 1). This possibility will be considered below after discussing observations made in Morrison Arm.

OBSERVATIONS IN MORRISON ARM

An interesting migration problem is presented by the Morrison deme smolts. To reach the outlet they must first swim in a SE direction and en route change to SW and W to move into the North Arm and then shift to NW to negotiate the northern section of the North Arm and Nilkitkwa Lake (Fig. 1). Extensive tagging operations in Babine Lake have shown that smolts from this deme are able to reach the outlet with equal success and cover similar distances per day as smolts from the other two demes (Johnson and Groot 1963). Morrison deme smolts must therefore change their migration direction over about 180° during their journey to the outlet.

Sonar observations on the migration of Morrison deme smolts were made on May 23–24 at the lower part of Morrison Arm (Fig. 1). The sonar barge was positioned along the shore of one of the small islands in this area looking east across the channel at a range of 124 m.

Figure 4C shows that smolt movements on the dates of observation occurred at dusk, stopped between 2300 and 2400 hr, and started again around 0100 hr, continuing through the dawn period and early morning hours. Only night and dawn periods show directional tendencies significantly different from uniformity at the 1% level (Fig. 7A). Dusk observations clearly indicate two modes and the mean direction for each mode has been determined separately.

In- and out-movements to the SW occurred during dusk, dawn, and night periods (Fig. 7A). This is the expected direction for migration on the most direct route to the outlet at the place of observation (Fig. 1). In addition, a strong N to NNE component is indicated for the dusk period. Simultaneous visual observations of near-surface migratory activity during this period on May 23 in Morrison Arm also indicated some movement in the opposite direction to the majority of schools (see Groot and Wiley 1965, Fig. 4). The northerly component during evening twilight can either be interpreted as "reversed migration" or it can be attributed to sockeye schools from the Main Lake population moving into Morrison instead of the North Arm. Main Lake observations near the entrance of Morrison Arm show a strong NNW to N tendency during the dusk period (Fig. 6B). These fish approaching the junction of arms will certainly end up in Morrison Arm if they continue on this course, and it is therefore conceivable that the northerly component found in Morrison Arm is the result of Main Lake smolts making the wrong choice of arm during their migration to the outlet. As mentioned before, some smolts tagged at the Sandspit trap in 1962 were recovered at the head of Morrison Arm.

Purse seining in July, after the migratory period, reveals very few smolts in Morrison Arm (Scarsbrook and McDonald MS 1970). Since only small numbers of two-year-old smolts leave the Babine Lake system, it is unlikely that Main Lake smolts, making the wrong choice, moved up into Morrison Lake (Fig. 1). Thus, Main Lake smolts diverted into Morrison Arm also get out again. It is possible that the SW directed movements at the Morrison Arm station are partly due to Main Lake smolts correcting their wrong choice by returning to the Old Fort area.

Smolts migrating out of Morrison Arm into the Main Lake have to turn clockwise at Old Fort Point to reach the outlet. Old Fort Point observations during the dawn period show strong SE swimming tendencies (Fig. 6C) and it has been suggested above that these could be smolts from Morrison Arm turning the wrong way, uplake instead of downlake.

OBSERVATIONS NEAR MCKENDRICK ISLAND

Tagging data show that smolts from both the Main and Morrison lakes demes do get into the North Arm when passing the junction of these three bodies of water near Old Fort (Johnson and

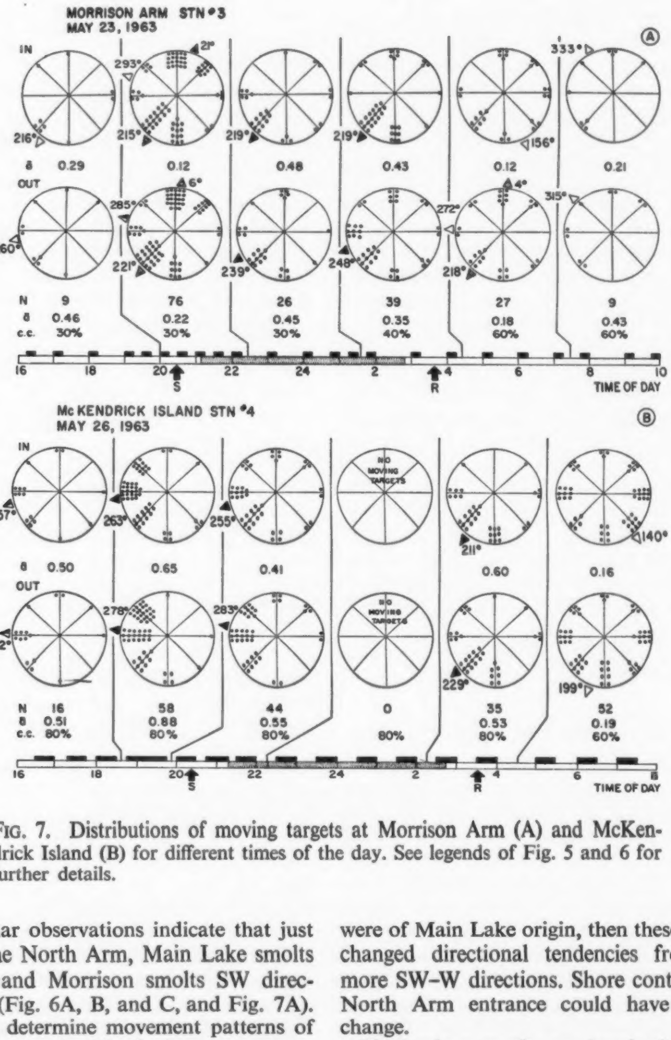

FIG. 7. Distributions of moving targets at Morrison Arm (A) and McKendrick Island (B) for different times of the day. See legends of Fig. 5 and 6 for further details.

Groot 1963). Sonar observations indicate that just before entering the North Arm, Main Lake smolts have NW to N and Morrison smolts SW directional tendencies (Fig. 6A, B, and C, and Fig. 7A). In an attempt to determine movement patterns of smolt schools close to the North Arm entrance, a sonar film was made at McKendrick Island on May 26. Scanning was in a southeastern direction over a range of 248 m. Direct movements in SW to W directions occurred during late afternoon, dusk, and dawn periods (Fig. 7B). Since in- and out-movements are very similar the smolt schools must have swum on rather direct courses.

As mentioned before, comparison of adult escapement numbers to Main and Morrison spawning grounds suggests that 14 times more Main than Morrison deme smolts should be migrating into the North Arm. If all smolts passing McKendrick Island were of Main Lake origin, then these fish must have changed directional tendencies from NW–N to more SW–W directions. Shore contour lines of the North Arm entrance could have enhanced this change.

If Morrison smolts are involved in the McKendrick Island observations, then the late afternoon and dusk observations indicate a westerly shift in movement (compare Fig. 7A and B). The similarity between the McKendrick dawn (211°N–229°N) and the Morrison night and dawn directions (219°N–248°N) is interesting to note. However, to be able to approach the McKendrick sonar station from a southwesterly direction, such Morrison smolts must also have followed a more westerly course to circumvent the north point of the North Arm entrance (Fig. 1). Since exact composition of Main and Morrison deme smolts passing the McKendrick sonar station is not known, it is impossible to verify the above speculations.

Concluding Comments

At the outlet sockeye smolts primarily migrate from the lake into the river at dusk and dawn. In the lake itself sonar observations often show movements at other times of the day. However, only during dusk, dawn, and early morning periods are directed movements evident, indicating that diel migratory activity in the lake also corresponds with the twilight periods. In Fig. 8, the in- and out-movements for these periods for all observation stations are presented.

In general, mean swimming directions correlate closely with the long axis of the bodies of water these fish were migrating through. At least during twilight, directions were toward the outlet but, if not, they tended to be almost exactly reversed. It is not possible at present to determine if these movements are caused by "reversed migration" or by smolts moving into the wrong arm or channel at the junction of bodies of water. Whatever the cause, these movements away from the outlet undoubtedly influence the progress of the demes as a whole during their migration out of the lake. However, nearly all smolts must get out of the Babine Lake system during the 1–1½-month migratory season, since very few (0.2%) leave as 2-year-olds (F. P. Jordan personal communication).

Morrison and Main lake smolts have to reach the outlet along different routes during the first part of their migration (Fig. 1). Figure 8 shows that smolts from these two demes swim in different directions which are generally appropriate for leaving the lake. In Morrison Arm smolts mainly move in a SW direction with some movement in N–NNE directions during dusk. In the Main Lake near Bear Island and close to the entrance of Morrison Arm movements are between NNW and NNE during twilight periods. At Old Fort, however, movements were predominantly in a SE direction, which is opposite from those expected. Near McKendrick Island, where both Morrison and Main lakes smolts must join, strong SW to W directions are evident. And, finally, further along the North Arm near Wolverine and Five Mile points, migration directions of Main Lake and Morrison Lake smolts are between NW and N. These findings in general support conclusions reached from previous studies in Babine Lake by Johnson and Groot (1963) and Groot (1965); namely, that in the uplake area of the Babine Lake system, we are dealing with two different groups of sockeye smolts, each with their respective migratory patterns. However, migration

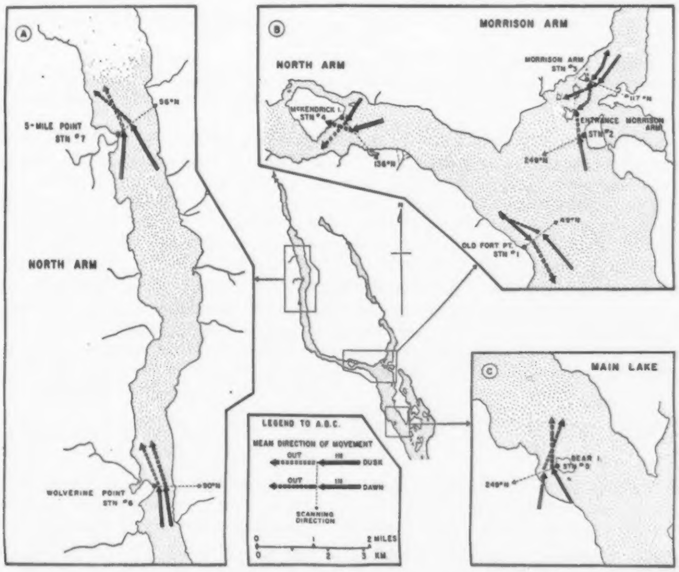
Ⓐ
96°N
5-MILE POINT
STN #7
NORTH ARM
WOLVERINE POINT
STN #6
90°N
Ⓑ
MORRISON ARM
NORTH ARM
MORRISON ARM
STN #3
117°N
McKENDRICK I.
STN #4
136°N
ENTRANCE MORRISON ARM
STN #2
249°N
49°N
OLD FORT PT.
STN #1
N
LEGEND TO A.B.C.
MEAN DIRECTION OF MOVEMENT
OUT
IN
DUSK
OUT
IN
DAWN
SCANNING DIRECTION
0
1
2 MILES
0
2
3 KM
Ⓒ
MAIN LAKE
BEAR I.
STN #5
249°N

FIG. 8. Mean directions of moving targets for in- and out-movements at dusk and dawn for different sonar film stations at Babine Lake.

towards the outlet may not proceed as smoothly as has been suggested in these two publications. Data presented here suggest possibilities of wrong choices or turns, which apparently are corrected again. Whatever guiding mechanisms lead these smolts to the outlet, determination of direction must be largely innate, since they are migrating for the first time through areas to a goal where they have never been.

Acknowledgments

I am much indebted to Mr W. L. Wiley for his assistance with the technical part of the work. Mrs N. Moffat is gratefully acknowledged for the many tedious hours she spent analysing the films frame by frame and for preparing the figures. Dr W. E. Johnson is thanked sincerely for the hospitality received at the Babine Lake field camps and for the many stimulating discussions on salmon migration problems.

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The Behavior of Adult American Shad (*Alosa sapidissima*) During Migration from Salt to Fresh Water as Observed by Ultrasonic Tracking Techniques

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DODSON, J. J., W. C. LEGGETT, AND R. A. JONES. 1972. The behavior of adult American shad (*Alosa sapidissima*) during migration from salt to fresh water as observed by ultrasonic tracking techniques. J. Fish. Res. Bd. Canada 29: 1445–1449.

Five of seven adult American shad (*Alosa sapidissima*), tracked continuously with ultrasonic transmitters in the lower estuary of the Connecticut River in 1968 during their spawning migration to fresh water, exhibited extensive meandering, ranging 24–53 hr in duration in the region of the saltwater–freshwater interface. The salinity in the Connecticut River is like a wedge; its daily position is dependent on upland discharge, and its hourly position is dependent on tidal activity. The fish were observed during all tidal conditions and at several discharge rates, and in all cases they remained near the leading edge of salt water during the meandering phase. This behavior pattern was not a result of handling nor was it a typical behavioral response to tidal cycle. It was concluded that the meandering observed in the region of the saltwater–freshwater interface was due to physiological adaptation of the fish to fresh water. Of the remaining two shad tagged, one proceeded directly upstream without meandering, and one moved downstream.

DODSON, J. J., W. C. LEGGETT, AND R. A. JONES. 1972. The behavior of adult American shad (*Alosa sapidissima*) during migration from salt to fresh water as observed by ultrasonic tracking techniques. J. Fish. Res. Bd. Canada 29: 1445–1449.

Des sept aloses savoureuses (*Alosa sapidissima*) suivies d'une façon continue à l'aide de transmetteurs ultrasoniques dans le bas estuaire de la rivière Connecticut en 1968 durant leur migration de fraie vers l'eau douce, cinq ont exécuté de vastes mouvements de va-et-vient, d'une durée de 24 à 53 h, à la limite entre l'eau salée et l'eau douce. La répartition de la salinité dans la rivière Connecticut est comme un coin, dont la position de jour en jour dépend du débit en provenance des hauteurs, et la position d'heure en heure dépend du balancement des marées. Les poissons, observés à tous les stades de marée et à plusieurs débits d'eau, demeurent, dans tous les cas, près du bord d'entrée de l'eau salée durant la phase de va-et-vient. Ce comportement n'est pas le résultat de la manipulation, non plus qu'une réaction typique au cycle de la marée. Nous en concluons que le mouvement de va-et-vient à la limite eau salée-eau douce est une conséquence de l'adaptation physiologique du poisson à l'eau douce. Des deux autres aloses marquées, une est entrée directement dans la rivière, sans va-et-vient, et l'autre s'est dirigée en aval.

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THIS paper describes the behavior of adult American shad (*Alosa sapidissima*) in the lower estuary of the Connecticut River during that stage of the spawning migration associated with the transition from salt to fresh water.

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The Connecticut River is New England's largest river, discharging an average of 19,500 ft^3/sec into Eastern Long Island Sound. Its mouth, constricted by a bedrock valley, is narrow. Because of its narrow mouth and large discharge, the salinity distribution in the lower river is a well defined "salt-wedge" (Meade 1966). This wedge consists of a narrow zone located several miles upstream of the river mouth where Connecticut River water mixes with salt water. The salinity wedge moves up and downriver in accordance with tidal rhythm. Water on the river bottom may contain 15‰ chloride at high tide but be almost completely fresh in the same region at low tide. The position of the salinity wedge is also sensitive to changes in upland discharge. The salinity wedge is depressed downstream by increasing discharge. This also results in a steepening of the salinity gradient in both the horizontal (downriver) and vertical directions, the most saline end of the gradient being respectively downriver and on the bottom. Migrating adult shad enter the Connecticut River in April and May when river discharge varies 60,000–14,000 ft^3/sec. At a discharge of 60,000 ft^3/sec the salt wedge extends less than 1 mile upriver and, at a discharge of 14,000 ft^3/sec, the salt wedge extends 6 miles upriver at high slack tide.

Materials and Methods

Seven adult shad were tagged internally with ultrasonic transmitters and tracked in the lower estuary of the Connecticut River during April and May, 1968. The sonic tags had a range of 100–2000 yards and an effective life of 2–3 weeks. Each tag was 2.5 inches in length, 0.5 inches in diameter, and weighed 0.5 oz in air. The receiving unit consisted of a portable battery-operated receiver tunable in the range 60KHZ–180KHZ, coupled to a hydrophone having a peak frequency of 70KHZ and a cone of reception of approximately 15°.

All fish were captured with 5½-inch (stretch measure) monofilament gillnets. Shad were removed from the net immediately upon capture and, if unharmed, were tagged by inserting a sonic tag into the stomach via the mouth. The fish were then gently returned to the water. Total time from capture to release was less then 1 min in all cases.

Fish were tracked continuously from an 18-ft outboard boat. The procedure involved maintaining the tracking boat in line with and directly behind the tagged fish, made possible by the directional characteristic of the hydrophone. The distance between fish and boat was estimated by changes in incoming signal strength. The position of the fish was obtained every 30 min by triangulation using navigational aids and prominent shore features as reference points. Fish position was plotted on enlargements of the navigation charts of the U.S. Coast and Geodetic survey. Tidal rate and direction were recorded coincident with each fish position.

No salinity observations were made in 1968 as no salinometer was available to us. To determine whether salinity was responsible for the observed movements, we predicted the salinity distribution in the lower estuary in 1968 using data obtained from the literature and salinity measurements made in the lower estuary in 1970 and 1971. Meade (1966) established that the position of the salinity wedge in the lower estuary of the Connecticut River is dependent on two major factors, upland discharge and tidal conditions. Salinity measurements were taken at high and low slack water on several days in the spring of 1970 and 1971 to determine the upstream extent of the salinity wedge (salinity>1‰). Daily discharge figures for 1970 and 1971 were obtained from the Thompsonville Gauging Station (located 70 miles up-river) of the U.S. Geological Survey, Water Resources Division. Discharge rates recorded at Thompsonville are followed a day later by equivalent changes in salinity at the mouth of the river (Meade 1966). The position of the upstream extent of the salinity wedge at high and low slack water was plotted together with the Thompsonville discharge reading for the previous day. Similar data obtained from Meade (1966) were also plotted, and curves were fitted to the points by eye (Fig. 1). Daily discharge values for 1968 were obtained from Thompsonville and the location of the upstream extent of the salinity wedge at high and low slack tide during the migrations of the tracked fish was read directly from Fig. 1 using the discharge rates for the day before the observations. The relation between the upstream position of the fish and the up-

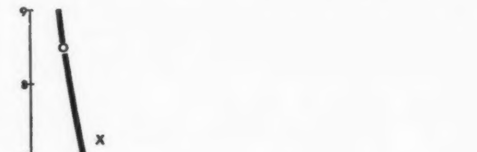

FIG. 1. Relation between river discharge, tide, and upstream extent of salt water in the lower estuary of the Connecticut River. The upper curve represents the leading edge of the salt wedge at high slack water. The lower curve represents the leading edge of the salt wedge at low slack water. X, points determined in this study (1970 and 1971); O, determined from Meade (1966).

stream position of the leading edge of the salinity wedge was examined by means of correlation analysis.

Comparisons were made between the behavior of migrating shad as revealed by this study and the behavior of shad migration exclusively in fresh water as revealed by the studies of Leggett and Jones (1967, 1968). The method and procedures used in both studies were similar.

Results

CHARACTERISTICS OF THE SALT WEDGE

The relation between discharge rates, tidal condition, and upstream extent of the salinity wedge in the lower estuary is illustrated in Fig. 1. The fish also experience a temperature change in passing from salt to fresh water. In early May, 1970, a 5 C increase in temperature coincided with reduction in salinity from 26‰ to 0‰. In mid-June of the same year, a 10 C increase in temperature coincided with reduction in salinity from 27‰ to 0‰. The observed increase in Δ T with time across the salinity wedge is due to a more rapid warming of river water relative to sea water.

Several other factors such as wind, deep holes, and islands affect the distribution of salinity in the lower estuary to a minor extent. These residual variations in salinity were not accounted for in our prediction of the upstream extent of the salinity wedge.

BEHAVIOR OF FISH

The behavior of five of the shad tracked in the lower estuary consisted of extensive meandering in the area of the upstream extent of salt water (Fig. 2). This movement resulted from a combination of passive drift and relatively inactive swimming. Leggett and Jones (in preparation) found the mean swimming speed of shad tracked in fresh water during 1967, 1968, and 1969 to be 2.1 ft/sec ($n = 401$, $\text{SD} = 1.3$). Dodson et al. (1970) found the mean swimming speed of shad tracked in Long Island Sound in salt water (28‰) during 1970 to be 2.5 ft/sec ($n = 416$, $\text{SD} = 1.4$) and during 1971 to be 2.4 ft/sec ($n = 470$, $\text{SD} = 1.2$) (Dodson et al. 1971). In comparison, the mean swimming speed for fish tracked in the lower estuary in this study was 1.3 ft/sec ($n = 159$, $\text{SD} = .98$). This represents a significant reduction of swimming speed in the saline reaches of the river compared to both fresh ($P < .01$) and salt ($P < .01$) water. The fish were rarely observed to outswim the tide when oriented into it. Thus the fish were passively maintained near the leading edge of the salt wedge. Fish 1 was tagged 1.5 miles above the leading edge of the salt wedge and meandered for 53 hr (Fig. 2). During this interval the fish maintained itself close to the upper limit of the salt water wedge (Fig. 3A). Similar behavior was observed in four other shad. Fish 2 was captured at the leading edge of the salt wedge. After 37 hr meandering in the lower estuary (Fig. 3B), a direct upstream migration of 13 miles in 8 hr occurred. Fish 3 was captured 1¼ miles below the upstream extent of salt water. The fish immediately migrated 3 miles upriver into fresh water where meandering behavior began and continued for 17 hr (Fig. 3C,1). Following this behavior, a direct upstream migration of 6 miles in 6 hr occurred. In all three cases, direct upstream migration occurred in fresh water and was continuous during periods of zero and reverse flow resulting from tidal action. Fish 4 (Fig. 3C,2) and Fish 5 (Fig. 3D) showed similar meandering behavior in the vicinity of the upstream extent of salt water but were lost before upstream migration occurred.

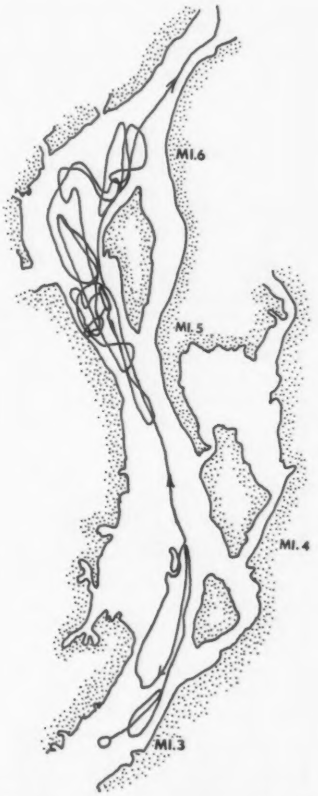

FIG. 2. The path of shad 1, tagged in the lower estuary of the Connecticut River at mile 3. This segment of the track lasted 45 hr. A further 8 hr of milling occurred in the vicinity of river mile 7 before continuous upstream migration occurred. See also Fig. 3A.

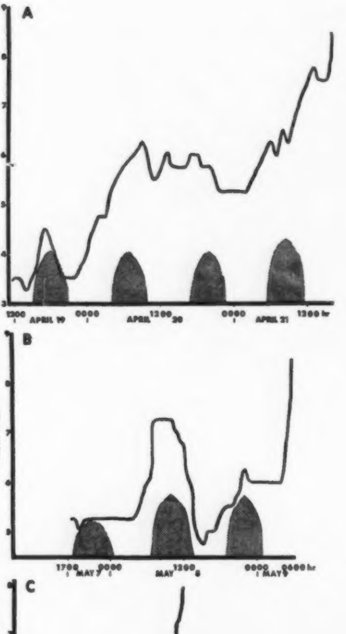

FIG. 3. A, The relation between the upstream displacement of shad 1 and the upstream extent of salt water at high and low slack water. The solid line represents the upstream displacement of the fish. Stippled area represents salt water. B, The relation between the upstream displacement of shad 2 and the upstream extent of salt water at high and low slack water. The solid line represents the upstream displacement of the fish. Stippled area represents salt water. C, (1) and (2), The relation between the upstream displacement of shad 3 and shad 4 and the upstream extent of salt water at high and low slack water. The solid lines represent the upstream displacement of fish. Stippled area represents salt water. D, The relation between the upstream displacement of shad 5 and the upstream extent of salt water at high and low slack water. The solid line represents the upstream displacement of the fish. Stippled area represents salt water.

The subsequent upstream migration of these two fish was confirmed with data obtained from an automatic shore-based ultrasonic tag monitor located at river mile 7. Fish 4 moved upstream past the monitor at 1800 hr on May 9, 71 hr after tagging. Fish 5 moved upriver past the monitor for the final time at 0936 hr on April 25, 64 hr after tagging. The displacement of these 5 fish from the mouth of the river at the time of high and low slack water was positively correlated with the upstream extent of the salt wedge at these times ($r = .682$, $n = 27$, $P < .001$).

Of the remaining 2 shad, Fish 6 was tagged $1\frac{1}{4}$ miles above the leading edge of the salinity wedge and migrated 20 miles continuously upstream in 20 hr. Fish 7 was tagged 3 miles below the upstream extent of salt water and, after 10 hr of holding its position, it migrated downstream into Long Island Sound.

Discussion

The extensive meandering of 5 of 7 shad in the lower estuary could have resulted from three factors: (a) atypical behavior due to physiological shock resulting from handling; (b) normal behavioral response to the tidal cycle; or (c) behavioral response to the transition from salt to fresh water.

The observed meandering does not appear to be a result of handling. Fish 3 was tagged 1.5 miles below the leading edge of the salt wedge and migrated 3 miles upstream in 5 hr. Only then did it begin to meander in the vicinity of the upstream extent of the salt wedge. We would expect meandering to occur shortly after release if handling produced physiological shock. Leggett and Jones (1968) reported that 13 of 16 shad tagged in fresh water, and followed for more than 5 hr after tagging, resumed their upstream migration within 4 hr. In contrast, this study has shown that in the vicinity of the leading edge of the salinity wedge, meandering behavior of 5 of 7 fish exceeded 12 hr.

Similarly, meandering in the lower estuary does not appear to be a response to tidal cycle. Fish 1, 2, and 3 were tracked in the lower estuary and in fresh water. In each case, extensive meandering occurred in the lower estuary whereas, in fresh water, upstream migration was continuous through conditions of zero and reverse flow due to tidal action. Leggett and Jones (1968) tracked two shad in fresh water within the tidal reach of the Connecticut River. Neither shad exhibited movement related to any stage of the tidal cycle. Similarly, 9 of 10 fish tracked in 1969 in fresh water showed no obvious changes in behavior related to tidal conditions (Leggett and Jones in preparation).

Two shad tracked in the lower estuary exhibited different behavior. Fish 7 returned to Long Island Sound after tagging. This fish was caught 3 miles below the leading edge of the salt wedge and may not have begun adaptation to fresh water at the time of capture. Fish 6 migrated upstream without hesitation.

We conclude that the observed meandering behavior of 5 of 7 shad tracked in the lower estuary of the Connecticut River is a consequence of the transition from salt to fresh water. The reactions of shad to specific salinities are not known as it is not possible to furnish accurate data on what salinity the fish were exposed to during the tracks. The prediction of the upstream extent of salt water is approximate and does not permit exact calculations of salinity values coincident with fish position. Furthermore, the position of the fish in the vertical salinity gradient is unknown as the ultrasonic tracking technique does not furnish information on fish depth.

Parry (1966), Milton (1971), and Bentley (1971) reviewed the literature on the physiological adaptations associated with the transition from salt to fresh water. Such a transition involves a number of changes in the osmotic composition of fish body fluid. The period of equilibration lasts for about 48 hr in eels and flounder transferred from fresh to salt water and 170 hr in steelhead trout (Bentley 1971). These times, however, represent the physiological equilibration period. No such data is available from the literature on the behavioral consequences of the transition from salt to fresh water or from fresh to salt water.

Tagatz (1961) showed that abrupt transfers of adult American shad from salt to fresh water caused some mortality where temperature was not a factor. Apparently shad must adapt slowly to fresh water. Those of our experimental fish tracked into fresh water meandered 24–53 hr at the leading edge of salinity. Automatic monitor data extended the maximum milling time to 71 hr. These time differences may have resulted from differences in the stage of fresh water adaptation attained by each fish at the time of capture.

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Crustacean Plankton and the Eutrophication of St. Lawrence Great Lakes

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Patalas, K. 1972. Crustacean plankton and the eutrophication of St. Lawrence Great Lakes. J. Fish. Res. Bd. Canada 29: 1451–1462.

Fourteen copepod and 13 cladoceran species were found in the summer plankton of lakes Superior, Huron, Erie, and Ontario. *Cyclops bicuspidatus thomasi* was the most abundant species in lakes Huron, Ontario, and Erie, and *Diaptomus sicilis* in Lake Superior. A general trend was seen from oligotrophic Lake Superior to eutrophic Lake Erie: the diminishing significance of calanoids (*Diaptomus sicilis* and *Diaptomus ashlandi*) accompanied by the increasing predominance of cyclopoids and cladocerans (*Cyclops bicuspidatus thomasi, Mesocyclops edax, Daphnia retrocurva, Daphnia galeata mendotae, Bosmina longirostris*, and *Bosmina coregoni coregoni*). The average crustacean abundance varied from 43 individuals/cm^2 in Lake Superior to 400/cm^2 in Lake Erie, and was related to both the heat and chlorophyll content of the water.

Total phosphorus loadings for the five Great Lakes were calculated using Vollenweider's criteria based on phosphorus exports from soils and human population densities in the drainage basins. They amounted to 0.03 g total P/m^2·year for Lake Superior, 0.15 for Lake Huron, 0.29 for Lake Michigan, 0.86 for Lake Ontario, and 0.98 for Lake Erie. The lake-average summer chlorophyll-*a* concentrations as well as Secchi disc visibilities were closely related to the phosphorus loading rates. Crustacean abundance was then indirectly related to the phosphorus loading rates. Based on the correlations found, predictions were made about changes in Secchi disc visibility and chlorophyll concentration with increasing human population densities in the drainage basin.

Patalas, K. 1972. Crustacean plankton and the eutrophication of St. Lawrence Great Lakes. J. Fish. Res. Bd. Canada 29: 1451–1462.

Nous avons identifié 14 espèces de copépodes et 13 de cladocères dans le plancton estival des lacs Supérieur, Huron, Erié, et Ontario. *Cyclops bicuspidatus thomasi* est l'espèce prédominante des lacs Huron, Ontario, et Erié, alors que dans le lac Supérieur, *Diaptomus sicilis* est le plus abondant. On décèle une tendance générale du lac Supérieur, qui est oligotrophe, au lac Erié, qui est eutrophe: l'importance décroissante des calanoïdes (*Diaptomus sicilis* et *Diaptomus ashlandi*) accompagnée d'une augmentation des cyclopoïdes et des cladocères, *Cyclops bicuspidatus thomasi, Mesocyclops edax, Daphnia retrocurva, Daphnia galeata mendotae, Bosmina longirostris* et *Bosmina coregoni coregoni*. L'abondance moyenne des crustacés varie de 43 individus par cm^2 dans le lac Supérieur à 400 dans le lac Erié et est liée à la température aussi bien qu'à la teneur en chlorophylle de l'eau.

Nous avons calculé la charge de phosphore total dans les cinq Grands lacs, nous servant du critère de Vollenweider basé sur les apports de P des sols et sur la densité des populations humaines dans les bassins hydrologiques. La charge de P s'élève à 0.03 g/m^2·an dans le cas du lac Supérieur, 0.15 pour le lac Huron, 0.29 pour le lac Michigan, 0.86 pour le lac Ontario, et 0.98 pour le lac Erié. La concentration estivale moyenne de chlorophylle-a, tout comme la visibilité du disque de Secchi, sont intimement liées au taux de charge de P. Indirectement, il en est ainsi de l'abondance des crustacés. A partir de ces corrélations, il est possible de prédire les variations de visibilité du disque de Secchi et de teneur en chlorophylle-a en fonction de l'accroissement de la densité des populations humaines dans le bassin hydrologique.

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Lakes Superior, Huron, Erie, and Ontario are affected to different degrees by progressing eutrophication. Among the most significant factors determining the degree of eutrophication within these lakes are the human populations inhabiting the basin (densities ranging from 7 inhabitants/km^2 in the Lake Superior basin to 153/km^2 in the Erie basin) and the different mean depths of these lakes

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(from 148 m in Lake Superior to 17 m in Lake Erie). Previous limnological studies have revealed a number of pronounced changes in chemistry and biology in some of these lakes during the past 60 years (Beeton 1965, 1969; Davis 1966).

The present investigation was undertaken to determine the species and abundance of crustacean zooplankton of the above mentioned lakes during the summer months and to look for their possible relations with temperature and eutrophication. Although much variation could be expected in the zooplankton composition in various seasons, the summer aspect of the community seems to be the most indicative and the most suitable for comparison. It reflects the period when all lakes usually reach their maximum temperature and maximum production. The paper is a continuation of the study initiated in 1967 on Lake Ontario (Patalas 1969) as part of the program developed by the Canada Centre for Inland Waters at Burlington, Ontario, in conjunction with the Fisheries Research Board of Canada.

Materials and Methods

Plankton samples were taken as vertical net hauls (Wisconsin-type monofilament nylon gauze: 25 cm in diameter and 77-μ mesh size in lakes Ontario, Huron, Superior; 12 cm in diameter and 90-μ mesh size in Lake Erie) from 50 m to the surface, or from the bottom to the surface in stations shallower than 50 m. The sampling was carried out at 32–60 stations per lake (Fig. 1) June 12–16, July 10–13, and August 5–8, 1967, on Lake Ontario; June 15–19 and July 29–August 3, 1968, on Lake Erie; August 5–13, 1968, on Lake Huron; and August 16–28, 1968, on Lake Superior. The samples were preserved in 2% formaldehyde. At least 200 specimens were counted and identified from each sample.

Zooplankton abundance was expressed as the number of specimens/cm^2 of lake area, copepod nauplii and cladoceran juveniles included, assuming that the filtration efficiency of the net was 100%. The data should not be

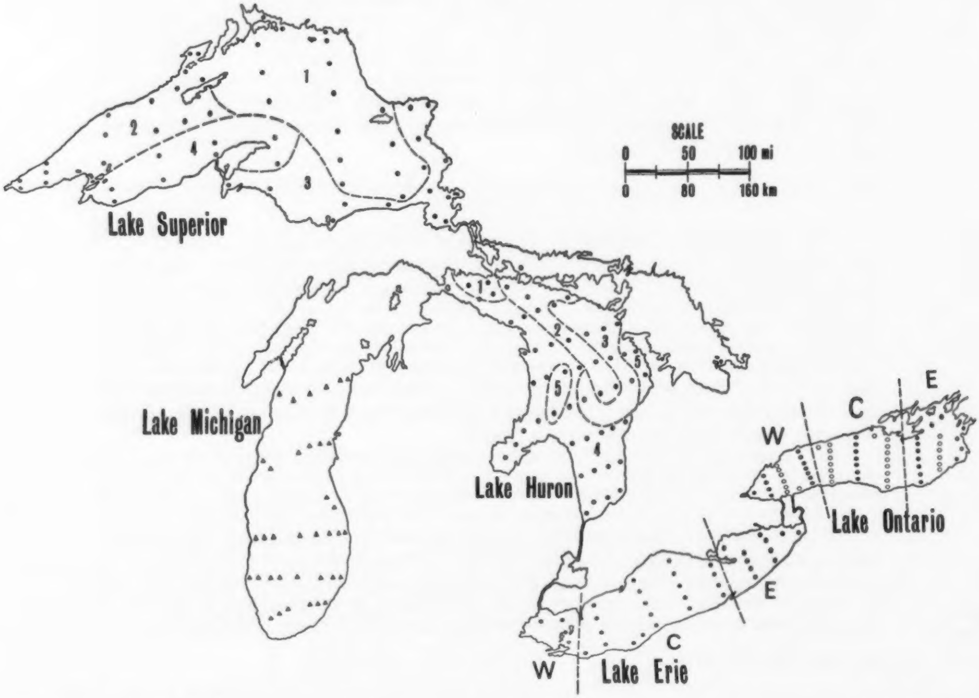

FIG. 1. Distribution of sampling stations in the Great Lakes. Solid circles: zooplankton sampling stations in August 1968 in lakes Superior and Huron; in June and July–August 1968 in Lake Erie; and in June, July, and August 1967 in Lake Ontario. Open circles, further Ontario stations sampled in July 1967. Black triangles on Lake Michigan: sites of Ayers et al. (1967) Secchi disc measurements. Dashed lines divide the western (W), central (C), and eastern (E) parts of lakes Erie and Ontario. Numerals on lakes Superior and Huron: areas differing in heat content (Table 1).

interpreted as true densities but rather as relative abundance values since the true efficiency of the net probably varied from 40–50% (Rawson 1956). The cruises were continuous and samples were taken throughout the 24-hr period. An analysis of the zooplankton data showed no significant relation between the abundance of most species and the time of sampling except for *Limnocalanus macrurus* and *Diaptomus sicilis*, whose numbers were underestimated because of migration below 50 m during daylight (Patalas 1969). Another limitation was a possible underestimation of the abundance of *Senecella calanoides*, which usually inhabits layers deeper than 50 m.

Temperature, Secchi disc visibility, and chlorophyll-*a* concentration in the surface water were taken from Anon. (1970a, b, c) and also, in part, from Nicholson (1970). As chlorophyll-*a* concentrations given in these reports were derived indirectly from fluorescence measurements (Lorenzen 1966), the results can be considered only as rough approximations.

Lake Erie was considered to consist of three distinct parts following Davis' (1968) arbitrary division into western, central, and eastern basins. The maximum depths of these three basins are: 16.5 m, 25.6 m, and 64 m, respectively (Wright 1955), and they contribute approximately 15, 60, and 25% to the total area, respectively.

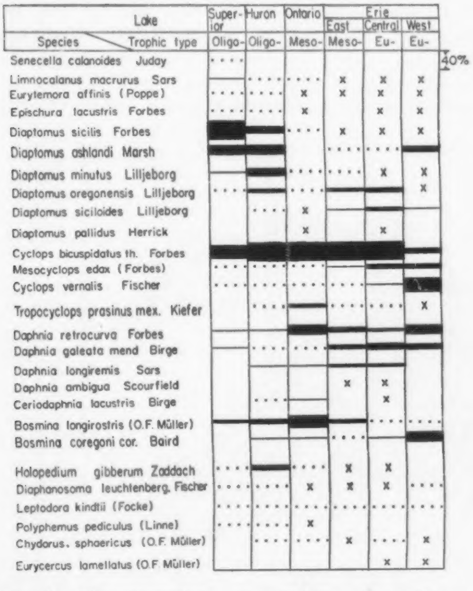

FIG. 2. The percentage composition of crustacean plankton in the four lakes in August 1967 and 1968. The heights of the bars are proportional to the percentages. Dots indicate a frequency below 1%; crosses denote that the species were found in the lake in summer months other than August.

Species Composition

Twenty-seven species of crustaceans were found in the summer plankton of the four lakes (Fig. 2); 14 were copepods and 13 were cladocerans. Nine of the copepods and six of the cladocerans were common to all four lakes, and 11 of the copepods and 10 of the cladocerans were common to lakes Huron, Erie, and Ontario. In spite of the general similarity of the species composition, particular species differed in relative abundance in the various lakes.

The crustacean plankton of Lake Superior was dominated mainly by diaptomids (*Diaptomus sicilis* and *Diaptomus ashlandi*) and the cyclopoid *Cyclops bicuspidatus thomasi*. Eleven of the 18 species of crustaceans were copepods. The percentages of *Limnocalanus macrurus* and *D. sicilis*, as indicated earlier, are certainly underestimated. Only seven cladoceran species were found in Lake Superior, three of them in very small numbers; the most abundant was *Bosmina longirostris*.

Lake Huron showed a similar distribution of species dominated by *C. bicuspidatus thomasi*, *D. sicilis*, *D. ashlandi*, and *D. minutus*. However, more cladoceran species were found here than in Lake Superior, the most abundant being *Holopedium gibberum* and *Bosmina longirostris*. The total number of crustacean species was 23 (12 copepods and 11 cladocerans), the largest number of species among the four lakes and very close to the total of 27 species found in the four lakes together.

Lake Ontario plankton was dominated by *C. bicuspidatus thomasi*, then in decreasing order by *B. longirostris*, *Daphnia retrocurva*, and *Tropocyclops prasinus mexicanus*. Diaptomids were represented by small numbers of *D. oregonensis*, *D. minutus*, *D. sicilis*, and very few specimens of *D. siciloides*. A few specimens of *D. pallidus* were found in October. A striking feature was the absence of *D. ashlandi* — a species present in all other St. Lawrence Great Lakes. The total number of species found in August was 18, but a few rare species found in spring and autumn brought the total for the study to 23.

The most abundant species in the east and central basins of Lake Erie was *C. bicuspidatus thomasi* followed in decreasing order by *D. galeata mendotae*, *D. retrocurva*, *B. longirostris*, *D. oregonensis*, *M. edax*, *D. longiremis*, and *D. siciloides*. The characteristic feature of the shallow western part was the very high abundance of *C. vernalis* in August, higher than that of *C. bicuspidatus thomasi*, *B. coregoni coregoni*, *D. retrocurva*, *D. galeata mendotae*, and *M. edax*. The total number of species found in the entire lake in August was 16, but the rare species found in spring and autumn brought the total for the study to 25.

When the lakes were arranged in order from oligo- to eu-trophic types (Fig. 2), a general trend was seen from Lake Superior, the most oligotrophic, to Lake Erie, the most eutrophic: a diminishing proportion of calanoids accompanied by an increasing predominance of cyclopoids and cladocerans.

Senecella calanoides was found only in Lake Superior, although this species could be expected also in Lake Huron (Carter 1969) and possibly in Lake Ontario if deeper hauls had been made.

Diaptomus sicilis was the most numerous species in Lake Superior and it decreased in relative abundance with increasing eutrophication of the lakes. A similar tendency was seen with *L. macrurus*. Even though its abundance was underestimated in lakes Superior, Huron, and Ontario; it was certainly absent in Lake Erie in August, since the majority of net hauls were taken from the bottom to the surface. A few specimens were found in June and July.

Cyclops bicuspidatus thomasi was the most abundant species in lakes Huron, Ontario, and Erie, although in the western part of Lake Erie *C. vernalis* was more numerous.

Bosmina coregoni coregoni, *D. galeata mendotae*, *M. edax*, *C. vernalis*, and *D. siciloides* were abundant only in Lake Erie, particularly in its western basin. Contrary to expectation, *D. longiremis*, known rather as a northern species typical of oligo- and meso-trophic lakes, was most abundant in eastern and central Lake Erie.

Crustacean Abundance in Relation to Temperature and Food

Temperature and food are considered to be two of the most important factors controlling zooplankton abundance in lakes. Temperature controls crustacean growth and hatching rates (Elster 1954, Eichhorn 1957). The availability of food affects the fertility of females (Edmondson 1965, Comita and Anderson 1959), thereby indirectly affecting the birth and mortality rates of the population. The precise evaluation of the food supply for zooplankton is a very complex matter if the various feeding mechanisms and sizes of different animals are considered (e.g. selective filtration, predation). However, a simplifying assumption can be made that the amount of food available to zooplankton is proportional to the concentration of chlorophyll or to the Secchi disc visibility, which in lakes of similar color is a function of the amount of suspended particles (primarily phytoplankton) in the upper water layers.

To investigate whether a relation existed between crustacean abundance and heat content on one hand and food supply on the other, crustacean numbers were plotted on a heat–food coordinate system (Fig. 3). Heat content (Table 1) was expressed as the number of kilogram calories within

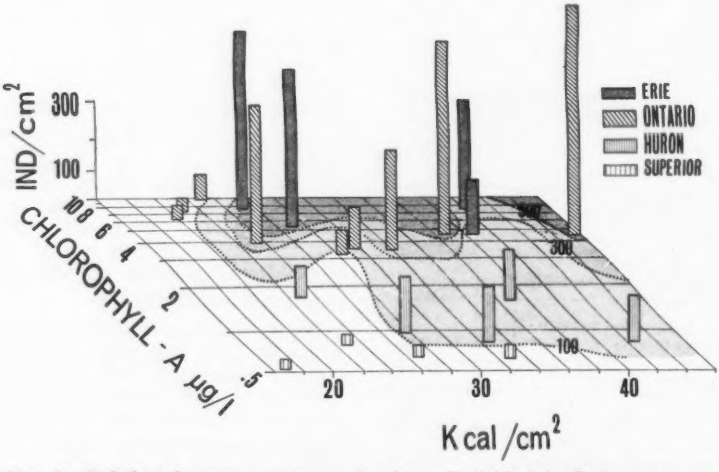

FIG. 3. Relations between crustacean abundance (individuals/cm^2), heat content (kcal/cm^2) and chlorophyll-*a* concentration in surface waters (µg/liter) for the four lakes. The bars represent mean crustacean abundance in different parts of the lakes: in June, July, and August for lakes Ontario and Erie and during August for lakes Superior and Huron. Dotted lines are isolines for crustacean abundance.

TABLE 1. Average heat contents of the 0–25 m layer calculated from a base of 0 C, chlorophyll-*a* concentrations in surface water, Secchi disc visibilities, and crustacean abundance calculated for particular lake basins in June, July, and August for lakes Ontario and Erie and in August for areas of lakes Huron and Superior differing in heat contents (shown in Fig. 1). Lake averages after areal weighting.

Area	Dates	Heat content (*kcal/cm²*)	No. of samples	Chlorophyll-*a* µg/liter	No. of samples	Secchi disc (*m*)	No. of samples	Crustaceans /cm²	No. of samples
				Erie					
East basin	June 15–16, 68	25.8	7	7.4	18	2.0	11	607	7
	July 29–30, 68	39.9	8	7.2	17	4.5	12	351	8
Central basin	June 17–19, 68	26.6	8	5.1	35	2.4	22	537	8
	July 30–Aug. 2, 68	38.5	9	4.7	43	3.6	25	214	9
Western basin	June 17–19, 68	.		20.3	3	.		.	
Average	Aug. 2, 68	.		11.4	8	2.0	1	.	
				7.0		2.9		400	
				Ontario					
East basin	June 15–16, 67	23.0	11	11.7	23	3.4	11	88	11
	July 12–13, 67	36.4	19	4.6	19	3.3	11	660	19
	Aug. 8–9, 67	45.5	13	4.4	18	3.3	10	800	13
Central basin	June 14–15, 67	20.0	7	6.2	41	3.9	15	59	7
	July 11–12, 67	29.4	24	3.5	22	3.6	15	164	24
	Aug. 6–7, 67	31.9	7	3.5	23	3.0	16	369	7
Western basin	June 12–13, 67	20.7	13	7.1	38	2.8	8	60	13
	July 10–11, 67	28.1	19	3.1	20	2.7	11	94	19
	Aug. 5–6, 67	23.2	12	3.7	19	2.9	14	465	12
Average				5.1		3.2		306	
				Huron					
1	Aug. 5–13, 68	22.6	3	1.7	3	.		86	3
2		27.7	8	0.9	7	9.2	6	186	8
3		32.5	8	0.7	7	8.2	6	178	8
4		36.6	13	1.5	7	7.4	14	164	13
5		42.5	5	0.7	3	3.6	10	174	5
Average				1.4		7.1		167	
				Superior					
1	Aug. 18–28, 68	17.4	15	0.5	15	9.2	15	38	15
2		22.6	8	0.8	8	7.8	10	39	8
3		27.0	8	0.6	8	7.9	8	48	8
4		32.5	12	0.6	12	7.8	6	49	12
Average				0.7		7.9		43	

a 0–25 m water column, 1 cm^2 in area, using 0 C as a base (Patalas 1969), and food conditions as the concentration of chlorophyll-*a* in near surface waters (Nicholson 1970).

In Lake Superior 38–49 crustaceans/cm^2 (mean 43 individuals/cm^2) were found with only slightly higher numbers in the warmest part of the lake. The chlorophyll-*a* contents were very low ranging 0.5–0.8 μg/liter.

Greater numbers, 86–186 individuals/cm^2 (mean 167 individuals/cm^2) were found in Lake Huron, where the chlorophyll-*a* concentrations were also higher, varying 0.7–1.7 μg/liter. The lowest crustacean density, 86 individuals/cm^2, was found in the coldest part of the lake (22.6 kcal/cm^2). In the remaining portions of the lake, the crustacean abundance did not vary substantially (164–186 individuals/cm^2) in spite of a wide range of heat content, 27.7–42.5 kcal/cm^2.

A wide range of crustacean abundance (59–800 individuals/cm^2, mean 306 individuals/cm^2) was found in Lake Ontario. Although the chlorophyll-*a* concentrations varied greatly (3.1–11.7 μg/liter), no correlation was found between chlorophyll-*a* and crustacean abundance within the lake. A significant correlation (r = 0.80) was found; however, between crustacean abundance and heat content (Patalas 1969). High chlorophyll-*a* values coupled with low temperatures were associated with low crustacean abundance.

A more complex situation existed in Lake Erie, 214–607 individuals/cm^2 (mean 400 individuals/cm^2) were found during the June and July–August periods, when the chlorophyll-*a* concentrations were relatively high, always above 4.7 μg/liter. Despite high chlorophyll-*a* concentrations, the crustacean numbers decreased in August as heat content increased. This might indicate that the temperature surpassed the range which in Lake Erie is optimal for maintaining high crustacean abundance, or that factors other than food (at least as represented by chlorophyll-*a* concentration) were operating.

Figure 3 suggests in general that both heat and food content controlled the crustacean abundance in the lakes under study, though in different ways. At low heat contents, the crustacean numbers were low and independent of chlorophyll-*a* concentration. With increasing heat contents in oligotrophic lakes Superior and Huron the crustacean numbers remained low and proportional to the low chlorophyll-*a* concentrations. With increasing heat content in mesotrophic Lake Ontario, where food was more abundant, an increase in crustacean numbers occurred. In the chlorophyll-*a* rich Lake Erie, after the heat content surpassed a seemingly optimum level, crustacean numbers dropped from a very high to a medium level. Similar midsummer decreases in numbers of zooplankton were frequently found in many meso- and eu-trophic lakes of Poland (Patalas 1954, 1963; Patalas and Patalas 1968).

Lake Eutrophication and Crustacean Abundance

The classical terms oligo-, meso-, and eu-trophy, in the sense of Naumann (1932) and Thienemann (1931), are useful in determining the general trophic characters of the Great Lakes, but they are inadequate for comparing them quantitatively. Åberg and Rodhe's (1942) definition of trophy, "the rate and ways of supplying a lake with organic matter," seems to be the most logical concept as it includes both autotrophy and allotrophy and considers the quantitative and dynamic aspects of the trophic phenomenon. Primary production is most frequently used as a uniform measure of autotrophy although it disregards allotrophy to some extent (Rodhe 1958, 1969), but it is difficult to obtain representative production data especially in bodies of water as complex as the Great Lakes. In an attempt to find a simple measure of eutrophication which is related to both autotrophic and allotrophic organic production, the concept of nutrient loading was developed by Vollenweider (1968, 1969). It was applied in this paper to explain the qualitative and quantitative differences in the crustacean plankton of the Great Lakes.

The total phosphorus loadings were calculated for lakes Superior, Huron, Ontario, Erie, and Michigan using Vollenweider's (1968) criteria. According to Vollenweider's estimates, the total phosphorus "export" from oligotrophic soils is <0.02 g total P/m^2 · year, from mesotrophic soils 0.02–0.05, and from polytrophic ones >0.05. Also, the contribution of total P by a human population inhabiting a representative basin area at a density of 150 inhabitants/km^2 amounts to 0.17–0.25 g/m^2 · year. Taking into account a high level of detergent use and intensification of North American agriculture, the upper value 0.25 g/m^2 · year was selected, corresponding to a load of 1.7 kg total P/capita · year. Phosphorus retention in the lakes was assumed to be 85% of the load based on calculations for Lake Erie (Anon. 1969).

The formula for total phosphorus loading (L_p in g total P/m^2 of lake surface · year) may be presented in the following form:[1]

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[1] The phosphorus supplied by precipitation was not included here. It can contribute significantly to the total P loadings for lakes in poor soil areas as demonstrated by Schindler and Nighswander (1970) and Armstrong and Schindler (1971).

$$L_p = E_s \cdot \frac{A_d}{A_o} + \frac{E_c \cdot C}{A_o} + 0.15\, L_{pa} \cdot \frac{A_o(a)}{A_o}$$

where: E_s = "Export" of phosphorus from the soil in g total P/m^2 of the land drainage · year.
A_d = Area of the land drainage in m^2
A_o = Area of the lake in m^2
E_c = Per capita discharge of phosphorus reaching the lake in g total P/capita · year.
C = Basin population
L_{pa} = Total P loading for the next lake upstream in g total P/m^2 · year.
$\frac{A_o(a)}{A_o}$ = Ratio of the area of the next lake upstream to the area of the lake considered.

The estimated total phosphorus loadings (Table 2) in g/m^2 of lake area · year were: Lake Erie 0.98, Lake Ontario 0.86, Lake Michigan 0.29, Lake Huron 0.14, and Lake Superior 0.03. There is good agreement between the estimated value of 0.98 g/m^2 · year for Lake Erie and the 1.06 g/m^2 · year measured directly (Anon. 1969). The corresponding figures for Lake Ontario (0.86 and 0.65 g/m^2 · year) also indicate a good agreement between estimated and measured values, suggesting that the estimated values for lakes Huron, Superior, and Michigan can be regarded as accurate within the limits of error usually associated with loading rate determinations.

The phosphorus loading, Secchi disc visibility, chlorophyll-*a* concentration, and crustacean abundance are presented here as lake-mean values thus averaging the great horizontal and temporal variations of these factors within the lakes (Davis 1969, Patalas 1969, Nicholson 1970, Edmondson 1972). This variation is due among other things to a very complex current pattern which results in water flowing in different directions at various depths (Anon. 1969). Unlike the phytoplankton, crustaceans

TABLE 2. Parameters used for calculation of the total phosphorus loadings for St. Lawrence Great Lakes.

	Symbol	Superior	Michigan	Huron	Erie	Ontario
Area of the lake in 10^6 m^2	A_o	82367[d]	58016[d]	59570[d]	25821[b]	19009[b]
Area of the land drainage in 10^6m^2	A_d	124838[d]	117845[d]	128464[d]	76790[b]	64229[b]
Ratio of land drainage to lake area	$\frac{A_d}{A_o}$	1.5	2.0	2.2	3.0	3.4
Basin population in millions	C	0.9[c]	7.5[c]	2.0[c]	11.8[b](6.0)[e]	6.1[e]
Export of phosphorus from the soil g tot.P/m^2 of land.year[a]	E_s	0.010	0.035	0.020	0.050	0.035
Per capita discharge of total phosphorus reaching lake, in g/year	E_c	1700	1700	1700	1700(1000)[e]	1700
(Calculations of loading in g tot.P/m^2 of lake·year)						
P loading from soil (Es.Ad/Ao)	1s	0.015	0.070	0.044	0.150	0.118
Population dependent P loading $\frac{E_c \cdot C}{(A_o)}$	1c	0.019	0.219	0.057	0.776(0.232)[e]	0.545
P loading from lake upstream (assuming 85% phosphorus retention in lake upstream) $(0.15\, L_{pa} \cdot \frac{A_o(a))}{A_o}$	1a	0	0	0.046	0.052(0.028)[e]	0.200
Total P loading from all sources (1s + 1c + 1a)	Lp	0.03	0.29	0.15	0.98(0.41)[e]	0.86

[a] Based on criteria from Vollenweider (1968).
[b] According to Anon. (1969).
[c] According to Beeton (1969).
[d] According to Chandler (1964).
[e] Calculated for Lake Erie for 1929. Population estimate according to Beeton (1969); E_c—reduced to 1000 g tot.P/capita·year taking into account no detergents in use.

change their vertical positions rhythmically over 24 hr, being passively carried in different horizontal directions during the day and night. Hence, the bulk of the crustaceans occupy a different water mass each day exploiting different algal aggregations. In such a situation, a low correlation, if any, could be expected between single values of chlorophyll, Secchi disc visibility, and crustacean abundance measured simultaneously at the same station. However, by using the averages of chlorophyll-*a*, crustacean abundance, and Secchi disc visibility from stations all over the lake, an apparent relation could be found. This was clearly demonstrated by Edmondson (1972), who found a good correlation between the summer mean transparency and mean chlorophyll in Lake Washington while single Secchi disc values plotted against chlorophyll concentrations gave widely scattered points. For the five lakes, a very high correlation coefficient ($r = -0.99$, $P = 0.001$) existed between the phosphorus loading and mean Secchi disc visibility (Fig. 4). Also, the chlorophyll-*a* concentration was closely related to the phosphorus loading ($r = 0.98$, $P = 0.01$). The mean crustacean abundance (Fig. 5) was a function of the mean chlorophyll-*a* concentration ($r = -0.97$, $P = 0.01$). However, a great variation in abundance of crustaceans within Lake Ontario also appears to have resulted from temperature effects (Fig. 3). The relation between crustacean abundance and the phosphorus loading ($r = 0.96$, $P = 0.01$) is simply a consequence of the relations found between phosphorus loading: chlorophyll-*a* and chlorophyll-*a*: crustacean abundance.

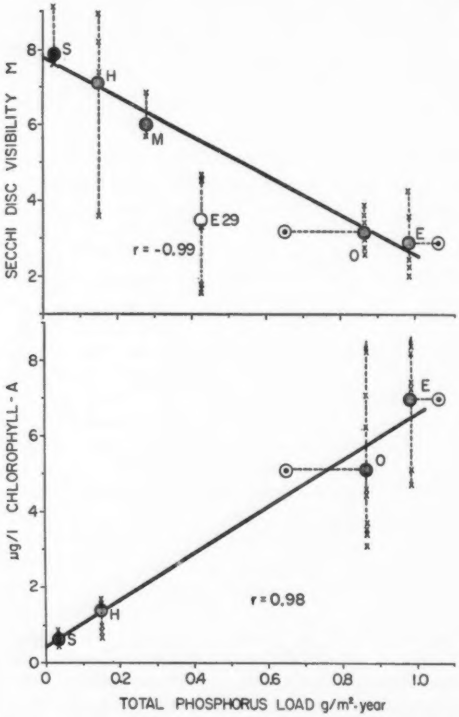

FIG. 4. Relation of lake-average Secchi disc visibility and chlorophyll-*a* concentration in surface water to total phosphorus loading for lakes Superior (S), Huron (H), Michigan (M), Ontario (O), and Erie (E). Darkened Total P loadings shown by darkened circles estimated according to Vollenweider's (1968) criteria; those by open circles with dots, Anon. (1969) estimates. Open circle (E 29) indicates 1929 values for Lake Erie, and crosses the ranges and mean values for chlorophyll-*a* and Secchi disc in particular basins or in parts of the lakes with different heat contents (Table 1).

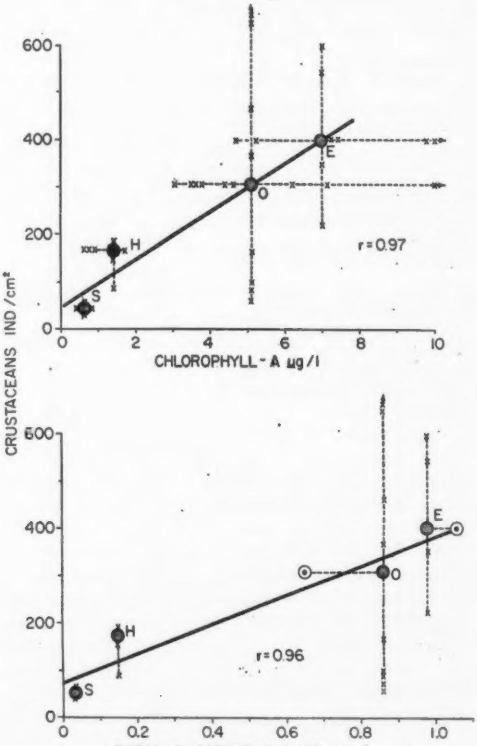

FIG. 5. Relations of crustacean abundance to lake-average chlorophyll-*a* concentration in surface water and total phosphorus loading for lakes Superior (S), Huron (H), Ontario (O), and Erie (E). Symbols as in Fig. 4.

Discussion

The very high number of species common to all the lakes under study seems to be a result of a similar postglacial history of the lakes, but differences in both the total abundance and the numerical role played by particular species in the community could be a reflection of the present morphological differences and chemical conditions of the lakes. In the last century rapidly growing human populations have had a greater modifying influence upon the chemical conditions of the aquatic environments (e.g. nutrients) than upon the physical ones (lake morphometry and related phenomena such as temperature, stratification), which probably did not change much during the last millenium. Since crustacean community development is related to both physical and chemical factors, a distinction has to be made between those characteristics of the planktonic community attributable to each group of factors.

A comparison of lakes Superior, Huron, and Ontario may provide this distinction. Although all three have great mean depths (148, 53, and 84 m, respectively) and all have cold, well oxygenated hypolimnia, as typical of oligotrophic lakes, they have widely differing phosphorus loadings (0.03, 0.15, and 0.86 g total P/m^2 · year, respectively). Hence, the differences in their crustacean communities can be attributed to their differences in nutrient loading. A declining proportion of diaptomids and an increasing abundance of cyclopoids (*C. bicuspidatus thomasi* and *T. prasinus mexicanus*) and cladocerans (*D. retrocurva*, *C. lacustris*, *B. longirostris*, and *B. coregoni coregoni*) are the more characteristic trends apparently related to increasing nutrients. On the other hand, comparison of lakes Ontario and Erie may provide an answer as to how lake morphology can affect the crustacean community. Lake Ontario has a mean depth five times as great as Lake Erie (86 and 17 m, respectively) but has a similar nutrient loading (0.86 and 0.98 g total P/m^2 · year, respectively). In Lake Erie, especially in the shallower western basin, *C. vernalis* and *M. edax* were more abundant than *C. bicuspidatus thomasi*, probably a result of the lesser depth and higher temperature of this lake (Andrews 1953, Davis 1968). Also, in the central and western basins, diminishing midsummer numbers of *B. longirostris* can be explained by the shallow depth and correspondingly warm hypolimnion. In Lake Ontario, the greatest abundance of *B. longirostris* preceded maximum water temperature (Patalas 1969). On the other hand, *B. coregoni coregoni*,[2] being abundant in the warmest part of Lake Ontario and in the central and western basins of Lake Erie, seems to prefer warmer waters rich in nutrients. In Polish lakes *B. coregoni coregoni* is typical for rather shallow, warm, eutrophic lakes (Patalas and Patalas 1966). The suggestion by Brooks (1969) and Goulden (1964) that *B. coregoni* could be considered as an indicator species for oligotrophic lakes refers to the subspecies *B. coregoni longispina* Leydig[3] (Patalas and Patalas 1966).

The high correlation coefficients for phosphorus loading vs. Secchi disc visibility, phosphorus loading vs. chlorophyll-*a* concentration (Fig. 4), and chlorophyll-*a* vs. crustacean abundance found in the group of lakes considered (Fig. 5) suggest that these interrelations might also be used to estimate some unknown parameters or to predict possible changes of these parameters in particular lakes. For example, no comparable information on lake average summer crustacean densities is available for Lake Michigan. Wells' (1960) data were collected with a net of a wide (220-μ) mesh and only from one station. Also, the data of Robertson (1968) and Swain et al. (1970), obtained with a continuous plankton recorder, are not comparable with the present data. Based on Fig. 5, one could expect in summer about 150 crustaceans/cm^2 on the average, a value corresponding to the Lake Michigan phosphorus loading of 0.29 g total P/m^2 · year. Similarly, a mean summer chlorophyll-*a* concentration of 2.0 μg/liter could be expected in Lake Michigan based on the total phosphorus loading (Fig. 4). Values within the range 0.8–2.6, on the average 1.26 μg/liter chlorophyll-*a*, were found by Saunders et al. (1962) in the north-eastern part of the lake during July–August, 1959 (Grand Traverse Bay). This value's being lower than the estimated 2.0 μg/liter is understandable since Saunders' measurements were taken more than 10 years ago and all samples were taken in the northern, more oligotrophic part of the lake, while the estimate refers to the lake average. Values close to the expected, on the average 1.9 μg/liter, were found in the central part of Lake Michigan in 1965 by Holland (1969).

The presented correlations could also be utilised to predict possible changes of some eutrophication-related parameters (e.g. Secchi disc visibility). Presuming that the population density in the Lake Ontario drainage basin increases from 6.1 million in 1966 to 7.6 million in 1986 as predicted (Anon. 1969) and that no remedial action towards the reduction of phosphorus in sewage is taken, the population-dependant phosphorus loading will rise from 0.54 to 0.69 g total P /m^2 · year, thus increasing the total loading to 1.0 g/m^2 · year (Table 2). As a result, the Secchi disc visibility in the lake could decrease from the present 3.2 m (Fig. 4) to about 2.6 m. However, if the plan to remove phosphorus from detergents (responsible for approximately 60% of P from human sources) is implemented, the total phosphorus loading would drop to about 0.5 g/m^2 · year and the Secchi disc visibility could be expected to increase to about 5.2 m on the average.

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[2] Synonym of *Eubosmina coregoni* (Baird) according to Deevey and Deevey (1971).

[3] Synonym of *Eubosmina longispina* (Leydig) according to Deevey and Deevey (1971).

This kind of prediction will probably be true for lakes Ontario, Michigan, Huron, and Superior as they have similar morphometry and such related phenomena as temperature and stratification. It may not, however, be true for Lake Erie, which is much shallower than the remaining Great Lakes and in which Secchi disc visibility may be a function not only of phytoplankton concentrations but also of suspended sediment particles, especially in the western basin. There are only a few direct evidences of transparency changes in the past in Lake Erie. Beeton (1969), comparing the changes in some chemical and biological characteristics of the Great Lakes during the last century, concluded that present information on past conditions does not offer any evidence of changes in the transparency of Lake Erie waters. He quoted Wright's (1955) data related to the west basin only. Another set of original Secchi disc measurements, carried out in the summer of 1929 in the central and eastern parts of Lake Erie by Green (1960), was carefully examined after selecting identical stations from the same months in which the measurements in 1968 were made by the CCIW staff in Burlington (Anon. 1970b). The lake average Secchi disc visibility for the months of June and late July or early August, 1929, was 3.4 m (i.e. 0.5 m higher than the data for 1968 which was calculated in the same way). It is difficult to say whether this difference indicates a long term trend or a year-to-year normal fluctuation. To relate the Secchi disc transparency of 1929 to the phosphorus loading of the same year, the calculation of the latter was carried out using the formula discussed in the previous section and amounted to 0.41 g total P/m^2 · year (Table 2). The basin population was estimated, according to Beeton (1969), as 6 million and the per capita discharge of phosphorus was assumed to be 1000 g/year taking into account that detergents were not used in 1929. The Secchi disc visibility observed in 1929 plotted against the phosphorus loading (Fig. 4) was much below the regression line based on the situation in the deeper Great Lakes, i.e. the visibility in Lake Erie was lower than could be expected in a deeper lake at a similar loading. This can be explained by the fact that the same load of phosphorus per unit lake area affects a shallow lake to a greater degree than a deeper one with a larger volume of water. Figure 6, originally constructed by Vollenweider (1968), serves as a good illustration of this relation.

Out of the five Great Lakes; Superior, Huron, and Michigan represent various stages of oligotrophy, and Lake Ontario is in the transitional stage between meso- and eu-trophy. Lake Erie, at present highly eutrophic, was already eutrophic in 1929, though closer to the mesotrophic range. Its position on the relative "scale" would suggest that a very drastic reduction of phosphorus input, possibly to below the 0.3 g/m^2 · year level, would be necessary to expect some apparent changes in the transparency of the water (Anon. 1969). On the other hand, it seems probable that Lake Ontario will respond quickly with an increasing transparency to the planned reduction of the phosphorus loading. Future, more precise investigation will indicate the extent to which these predictions are correct.

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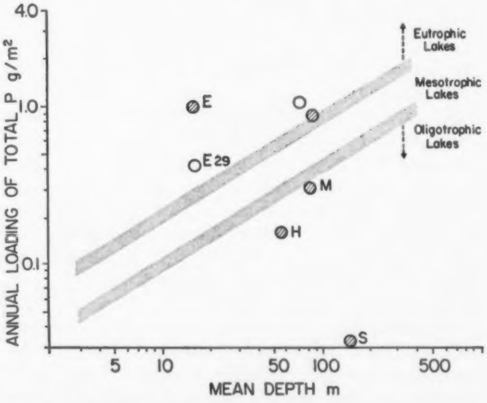

FIG. 6. Annual total phosphorus loadings for lakes Superior (S), Huron (H), Michigan (M), Ontario (O), and Erie (E) as related to the mean depths. The hatched circles refer to 1968 loadings, the open circle (E 29), to Lake Erie, 1929. Calculation of the loadings and definition of the trophic types by the diagonal lines based on Vollenweider (1968). Lakes plotted below the lower line are oligotrophic and those above the upper line are eutrophic. The vertical distance above the upper line can be considered as a measure of eutrophication.

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NOTES

Acute Zinc Toxicity to Rainbow Trout (*Salmo gairdneri*): Confirmation of the Hypothesis that Death is Related to Tissue Hypoxia

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BURTON, D. T., A. H. JONES, AND J. CAIRNS, JR. 1972. Acute zinc toxicity to rainbow trout (*Salmo gairdneri*): confirmation of the hypothesis that death is related to tissue hypoxia. J. Fish. Res. Bd. Canada 29: 1463–1466.

Acute heavy metal toxicity to fish has been attributed to the coagulation or precipitation of mucus on the gills and/or to cytological damage to the gills. The physiological mechanism of death by either of the above causes is related to a breakdown in gas exchange at the gills. This study of acute zinc toxicity to rainbow trout (*Salmo gairdneri*) supports an earlier hypothesis that modification of the gas exchange process at the gills creates hypoxia at the tissue level. Tissue hypoxia appears to be a major physiological change preceding death once the gas exchange process at the gills is no longer sufficient to supply the oxygen requirements of the fish.

BURTON, D. T., A. H. JONES, AND J. CAIRNS, JR. 1972. Acute zinc toxicity to rainbow trout (*Salmo gairdneri*): confirmation of the hypothesis that death is related to tissue hypoxia. J. Fish. Res. Bd. Canada 29: 1463–1466.

La toxicité des métaux lourds chez les poissons a été attribuée à la coagulation ou précipitation du mucus sur les branchies et/ou à la détérioration des cellules branchiales. Le mécanisme physiologique de la mort par l'une ou l'autre de ces causes est lié à une rupture des échanges gazeux au niveau des branchies. Notre étude sur la toxicité aiguë du Zn à l'endroit de la truite arc-en-ciel corrobore l'hypothèse que la modification du processus d'échanges gazeux cause une hypoxie des tissus. L'hypoxie tissulaire semble être un changement physiologique majeur précédant la mort, lorsque le processus d'échanges gazeux au niveau de la branchie ne réussit plus à fournir au poisson l'oxygène dont il a besoin.

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THE mode of toxicity of zinc and other heavy metals to fish has been studied since the mid-1920s (see reviews by Doudoroff and Katz 1953; Skidmore 1964). Early investigators such as Carpenter (1925, 1927, 1930), Dilling et al. (1926), Jones (1935, 1938, 1939), Ellis (1937), and Westfall (1945) attributed the death of fish exposed to lethal concentrations of heavy metals to the coagulation or precipitation of mucus on the gills which was thought to cause death by suffocation. More recently, Lloyd (1960), Skidmore (1970), and others have suggested that cytological damage to the gills rather than mucous accumulation causes death by asphyxia.

The physiological mechanism of death in these cases appears primarily to be related to a breakdown in gas exchange at the gills. Skidmore (1970) studied the changes in several respiratory parameters of rainbow trout (*Salmo gairdneri*) due to zinc sulfate toxicity. He pointed out that these changes are similar to those observed for trout and other fish which have been exposed to environmental conditions which produce hypoxia. Furthermore, Skidmore proposed that death in fish with gills damaged by heavy metals is probably caused by tissue hypoxia.

To test the hypothesis that death from acute heavy metal toxicity is related to tissue hypoxia, changes in lactic acid and pyruvic acid concentrations in skeletal muscle and liver tissue were measured when rainbow

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trout were exposed to a lethal concentration of zinc sulfate in water nearly saturated with oxygen.

Materials and methods — Rainbow trout (*Salmo gairdneri*) from the National Fish Hatchery at Paint Bank, Virginia, were acclimated to 15 ± 1 C for at least 15 days under the same laboratory conditions described by Burton and Spehar (1971). Average total hardness of the water used for acclimation and testing was 51 mg/liter as $CaCO_3$ (range, 37–54), mean methyl orange alkalinity was 38 mg/liter $CaCO_3$ (range, 35–44), and mean *p*H was 7.8 (range, 7.2–8.0). Mean dissolved oxygen concentration was 8.2 mg O_2/liter (range 7.7–8.6) except during the hypoxic stress experiments. Measurement procedures were as outlined in American Public Health Association et al. 1965.

A constant photoperiod of 12 hr light and 12 hr dark was maintained before and during testing. All fish were fed every 3 days with Purina Trout Chow Pellets. Fish were not fed for 48 hr preceding a test or during a test. The average weight of the trout, which included both sexes, was 100.9 g (range, 66.2–140.8), mean standard length was 181 mm (range, 115–208), and mean total length was 215 mm (range, 146–246).

Experimental procedures — The effects of zinc on changes in skeletal muscle and liver lactic acid and pyruvic acid concentrations were studied by exposing four groups of trout to four test conditions in an apparatus similar to the one described by Burton and Spehar (1971). Briefly, all tests were carried out with fish housed in Plexiglass cylinders (approximately 900 ml capacity; 6.5 cm ID × 27.5 cm long) which received a continuous flow (75 ± 5 ml/min) of constant temperature water (15±0.5 C). Once the water passed through the chambers it was discarded. To insure that no zinc was present at the beginning of each experiment, all Plexiglass cylinders were washed with detergent and water, wiped with a 0.1 N solution of ethylenediaminetetraacetic acid (EDTA), washed a second time with detergent and water and then rinsed with dechlorinated tapwater. The same procedure was used to clean all water lines, flow meters, and water baths after each set of experiments. A Norelco-Unicam SP90A Atomic Absorption Spectrophotometer was used to check for cleanliness and for all zinc analyses in this study.

Eleven trout tested in group 1 were held for approximately 20 hr in a continuous flow of water with no measurable zinc present and with dissolved oxygen concentrations near saturation. The fish were then exposed to a gradual increase in Zn^{++} from 0 to 40 mg Zn^{++}/liter (calculated as Zn^{++} from $ZnSO_4 \cdot 7H_2O$) in well oxygenated water until they died. The exposure to Zn^{++} was carried out by bleeding in water saturated with dissolved oxygen containing 40 mg Zn^{++}/liter over a 2-min period. A fish was considered dead when ventilation ceased for 30 sec. Tissues were taken for lactic acid and pyruvic acid analysis immediately at death by the procedure outlined by Burton and Spehar (1971).

In group 2, 11 control fish were held for approximately 24 hr in a continuous flow of water under the same conditions as fish in group 1, with the exception that no Zn^{++} was introduced. The fish were then removed, stunned by a blow on the head, and skeletal muscle and liver tissue samples were taken for lactic acid and pyruvic acid analysis.

Groups 3 and 4 (12 fish per group) were exposed to essentially the same conditions as fish in groups 1 and 2 with the exception that 10 mg M.S. 222/liter were added to the water. Because most of the trout struggled when the toxic solution was first introduced, these series of experiments were conducted to determine whether or not the changes being measured were due to struggling or tissue hypoxia. According to Skidmore (1970), this concentration of M.S. 222 in zinc free water is sufficient to calm rainbow trout and does not depress their rate of oxygen consumption or affect their balance or their reaction to visual stimuli.

Trout in group 3 were held 20 hr in a continuous flow of water. At this time, well oxygenated water containing 10 mg M.S. 222/liter was bled into the system over a 2-min period. These fish were subjected to 10 mg M.S. 222/liter for 0.5 hr. Next, water containing 40 mg Zn^{++}/liter plus 10 mg M.S. 222/liter was introduced over a 2-min period. Trout were held in this water until they died. At death, muscle and liver tissues were taken for analysis.

Control trout in group 4 were held for 20 hr and then exposed to well oxygenated water containing 10 mg M.S. 222/liter which was bled into the system over a 2-min period. The control trout in 10 mg M.S. 222/liter were held in this water up to 5 hr before tissues were taken for lactic acid and pyruvic acid analysis.

The effects of low dissolved oxygen on skeletal muscle and liver lactic acid and pyruvic acid concentrations were established by exposing 10 trout to gradual environmental hypoxia as described by Burton and Spehar (1971). Trout were held in the flow through Plexiglass cylinders at 15 ± 0.5 C for approximately 20 hr. Oxygen concentration was then lowered approximately 0.6 mg O_2/liter each half hour from 8.2 mg O_2/liter (pO_2 = 148 mm Hg) to 3.9 mg O_2/liter (pO_2 = 65 mm Hg) over a 4.5-hr period. Eleven control fish were treated similarly except that oxygen was held at approximately 8.2 mg O_2/liter. When removed from the Plexiglass cylinder both control and experimental fish were stunned by a blow on the head, and skeletal muscle and liver tissue samples were taken.

Statistical methods — The difference between treatment means of the control versus the experimental fish were tested statistically by an extension of Duncan's multiple range test to group means with unequal numbers of replications (Kramer 1956).

Results and discussion — Significant increases ($P < 0.01$) in lactic acid concentrations were found in both muscle and liver tissues when the experimental fish were compared to the controls in both the zinc stressed and hypoxic stressed fish (Table 1). A significant decrease ($P < 0.01$) was found in muscle pyruvic acid concentrations in trout exposed to a lethal concentration of zinc and hypoxia (Table 1). Trout killed by zinc had significant decreases ($P < 0.01$) in liver pyruvic acid concentrations in contrast to no significant changes ($P > 0.05$) in hypoxic stressed fish (Table 1).

These metabolic changes in both tissues, with the exception of the changes in liver pyruvic acid, are similar in rainbow trout exposed to either a lethal concentration of zinc or severe hypoxic stress and indicate a severe lack of oxygen at the tissue level. Holeton and Randall (1967) demonstrated in rainbow trout subjected to environmental hypoxia that a decrease in the partial pressure of oxygen (pO_2) occurred in the circulatory system as environmental oxygen concentrations were lowered. This decrease in circulatory pO_2 imposes hypoxia at the tissue level. Skidmore (1970) found that the pO_2 in dorsal aortic blood declined steadily following exposure of rain-

TABLE 1. A comparison of lactic acid and pyruvic acid changes (mg acid/100 g wet wt tissue) in skeletal muscle and liver of rainbow trout subjected to a lethal concentration of zinc and environmental hypoxia. Number of fish in parentheses.

		Zinc		Hypoxia	
		Control fish	Stressed fish	Control fish	Stressed fish
Muscle lactic acid	Mean	123.1	334.7[a]	108.2	242.6[a]
		(11)	(11)	(11)	(10)
	Range	85.3–181.8	270.8–398.6	57.0–164.4	91.5–367.3
Muscle pyruvic acid	Mean	2.7	1.0[a]	1.8	0.8[a]
		(11)	(11)	(11)	(10)
	Range	1.7–3.8	0.2–3.7	1.0–2.9	0.5–1.4
Liver lactic acid	Mean	14.6	127.3[a]	14.3	79.6[a]
		(10)	(11)	(10)	(10)
	Range	8.7–23.3	90.4–231.5	4.6–24.7	28.3–135.6
Liver pyruvic acid	Mean	0.7	0.5[a]	0.8	0.8[b]
		(10)	(11)	(10)	(10)
	Range	0.4–1.1	0.4–0.6	0.5–1.2	0.6–1.7

[a] $P < 0.01$.
[b] $P > 0.05$.

TABLE 2. A comparison of lactic acid and pyruvic acid changes (mg acid/100 g wet wt tissue) in skeletal muscle and liver of rainbow trout subjected to zinc and zinc + M.S. 222[a]. Number of fish in parentheses.

		Control fish	Control fish + M.S. 222	Zinc stressed fish	Zinc stressed fish + M.S. 222
Muscle lactic acid	Mean	123.1	134.6	334.7[a]	277.4
		(11)	(12)	(11)	(12)
	Range	85.3–181.8	33.4–227.0	270.8–398.6	141.6–335.6
Muscle pyruvic acid	Mean	2.7	2.6	1.0	1.2
		(11)	(12)	(11)	(12)
	Range	1.7–3.8	1.6–3.4	0.2–3.7	0.4–2.3
Liver lactic acid	Mean	14.6	16.6	127.3	71.2
		(10)	(12)	(11)	(12)
	Range	8.7–23.3	8.7–30.8	90.4–231.5	39.6–130.6
Liver pyruvic acid	Mean	0.7	0.8	0.5	0.5
		(10)	(11)	(11)	(11)
	Range	0.4–1.1	0.5–1.2	0.4–0.6	0.3–0.7

[a] Means not underscored by the same line are significantly different at $P < 0.01$. Others not significantly different.

bow trout to 40 mg Zn^{++}/liter in well oxygenated water indicating that hypoxia occurred at the tissue level. The results of the present study demonstrate that tissue hypoxia precedes death when maximum gill ventilation is no longer sufficient to supply the oxygen needs of trout because of gill damage which modifies gas exchange.

In the series of experiments designed to determine whether or not changes in muscle and liver lactic acid and pyruvic acid were due to exercise or tissue hypoxia, no significant difference ($P > 0.05$) was found in muscle and liver lactic acid and pyruvic acid concentrations in control fish with no anesthetic present and in control fish mildly sedated by 10 mg M.S. 222/liter (Table 2). When trout exposed to a gradual increase of zinc from 0 up to 40 mg Zn^{++}/liter with no anesthetic present were compared to calmed trout under the same test conditions, a significant difference ($P < 0.01$) was found in lactic acid concentrations of both muscle and liver (Table 2). Lactic acid concentrations were significantly higher in fish exposed to zinc with no anesthetic present. This showed that struggling contributed significantly to the total accumulation of lactic acid. However, a significant increase in lactic acid accumulation still occurred in calmed trout which did not struggle when the toxicant was introduced. We may, therefore, assume that an increase in lactic acid indicates severe tissue hypoxia. No significant differences ($P > 0.05$) were found in muscle and liver pyruvic acid concentrations when non-sedated and mildly sedated trout exposed to zinc were compared.

In summary, this study confirms Skidmore's (1970) hypothesis that gill damage modifies gas exchange and creates hypoxia at the tissue level. Tissue hypoxia appears to be a major physiological change preceding death when rainbow trout are exposed to acute zinc toxicity. Because other heavy metals similar to zinc appear to kill several species of fish by damaging their gills when they are exposed to acute concentrations of the metals (Doudoroff and Katz 1953; Skidmore 1964), we feel that death related to tissue hypoxia may also be occurring in these species.

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Oxidation of Lactate to Carbon Dioxide by Rainbow Trout (*Salmo gairdneri*) Tissues

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BILINSKI, E., AND R. E. E. JONAS. 1972. Oxidation of lactate to carbon dioxide by rainbow trout (*Salmo gairdneri*) tissues. J. Fish. Res. Bd. Canada 29: 1467–1471.

A comparative study on the ability of various fish tissues to carry out different stages of lactate oxidation was conducted with rainbow trout (*Salmo gairdneri*). Rate of oxidation of Na-L-lactate-1-^{14}C (5 mM) and Na-L-lactate-3-^{14}C (5 mM) by tissue slices from white muscle, red lateral line muscle, heart, liver, kidney, and gills was determined at 15 C by measuring the formation of $^{14}CO_2$. In all tissues the liberation of $^{14}CO_2$ was considerably higher with lactate-1-^{14}C than with lactate-3-^{14}C. Liver was the most active tissue for oxidation of lactate-1-^{14}C (2805 $m\mu$moles/g wet tissue/hr at 15 C) and gills for oxidation of lactate-3-^{14}C (556 $m\mu$moles/g wet tissue/hr at 15 C). With both substrates activity in the white muscle was very limited, whereas other tissues had an intermediate level of activity. The results suggest that, in trout, the catabolism of lactate may take place through oxidative decarboxylation of pyruvate and that liver plays an important role in such a process. It appears also that complete oxidation of lactate may be of significance in supplying energy for the exchange reactions in gills.

BILINSKI, E., AND R. E. E. JONAS. 1972. Oxidation of lactate to carbon dioxide by rainbow trout (*Salmo gairdneri*) tissues. J. Fish. Res. Bd. Canada 29: 1467–1471.

Les auteurs ont effectué sur la truite arc-en-ciel (*Salmo gairdneri*) une étude comparative de l'aptitude de divers tissus de poisson à oxyder le lactate. Mesurant la formation de $^{14}CO_2$, ils ont déterminé les taux d'oxydation du Na-L-lactate-1-^{14}C (5 mM) et du Na-L-lactate-3-^{14}C (5 mM) de tranches de tissus du muscle blanc, du muscle rouge de la ligne latérale, du coeur, foie, rein, et des branchies à 15 C. Dans tous les tissus, la libération de $^{14}CO_2$ a été beaucoup plus élevée avec le lactate-1-^{14}C qu'avec le lactate-3-^{14}C. Le tissu hépatique est celui qui oxyde le plus activement le lactate-1-^{14}C (2805 $m\mu$moles/g de tissu humide/h à 15 C), alors que le tissu branchial est le plus actif sur le lactate-3-^{14}C (556 $m\mu$moles/g de tissu humide/h à 15 C). L'activité du muscle blanc sur les deux substrats est très limitée. Les autres tissus ont une activité intermédiaire. Ces résultats suggèrent que le catabolisme du lactate chez la truite arc-en-ciel se produit par décarboxylation oxydative du pyruvate et que le foie jour un rôle important dans ce processus. Il semble de plus que l'oxydation complète du lactate soit une source d'énergie pour les réactions d'échange dans les branchies.

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THE metabolism of lactate has been the object of thorough investigation in fish in relation to the biochemical changes taking place during and following muscular activity (e.g. Dando 1969; Fraser et al. 1966; Tomlinson et al. 1961; Black et al. 1961). The enzyme lactate dehydrogenase, which mediates lactate–pyruvate interconversion, has been studied extensively in fish, particularly in relation to the generic and physiological significance of the occurrence of the different isoenzyme forms (Williscroft and Tsuyuki 1970 and references cited). After conversion to pyruvate, the carbon skeleton of lactate may follow various metabolic routes: it may serve for biosynthesis of glucose and glycogen (Cori and Cori 1928; Hostetler et al. 1969) or lipids (Katz et al. 1971) and undergo various degrees of oxidation, leading ultimately to the formation of CO_2 from one or more of the three carbons (White et al. 1968; Jorfeldt 1970). The formation of glycogen from lactate has been the subject of a number of investigations in fish (e.g. Bone 1966; Black et al. 1966; Pritchard et al. 1971) but, with the exception of the studies of Wittenberger (Wittenberger and Diaciuc 1965; Wittenberger 1968) on the metabolic functions of the red muscle, there is very little information available on the oxidative metabolism of lactate in fish. The purpose of our study was to compare the ability of various trout tissues to perform two different stages in lactate oxidation.

Material and methods — Rainbow trout (*Salmo gairdneri*) were obtained from Sun Valley Trout Farm at

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Mission, B.C. They were of both sexes and weighed 150–200 g. Fish were maintained under conditions described earlier (Bilinski et al. 1971). The fish used had not been fed for about 20 hr before being killed.

^{14}C-labelled lactate — Na-L-lactate-1-^{14}C and Na-L-lactate-3-^{14}C were obtained from New England Nuclear Corp., Boston, Mass. They were diluted with nonradioactive L-lactic acid (Sigma-grade L-1), converted to sodium salts, and adjusted to *p*H 7.4. The solutions, used as substrate, had the specific activities of 4000–5000 counts/min per μmole. We tested the radiopurity of lactate-1-^{14}C and lactate-3-^{14}C by chromatography on Whatman No. 1 paper, using the following solvent systems: ethanol:ammonium hydroxide(28%):water, 20:1:4 (Rf of lactic acid = 0.60) and *n*-butanol:formic acid (88%): water, 20:1:10 (Rf of lactic acid = 0.73). The distribution of radioactivity on paper chromatograms was determined by scintillation counting and it was found that all the radioactivity present occurred at the Rf of lactic acid.

Determination of lactate oxidation — The level of oxidative activity in various tissues was measured by the release of $^{14}CO_2$ from lactate-1-^{14}C or lactate-3-^{14}C. Unless otherwise stated, the techniques used for incubation, diffusion and recovery of $^{14}CO_2$, and determination of radioactivity by scintillation counting were the same as described previously in a study on fatty acid oxidation (Bilinski and Jonas 1970). Tissue slices were cut in a cold room at 0–4 C with a Stadie-Rigg slicer (Stadie and Rigg 1944) and weighed directly into Warburg flasks by pooling approximately equal weights of the tissue from three fish. The standard incubation mixture (2.0 ml) had the following composition (Brin et al. 1952): Na_2HPO_4-NaH_2PO_4, 20 mM, *p*H 7.4; NaCl, 115 mM; KCl, 4 mM; $MgCl_2$, 5 mM; Na lactate-1-^{14}C or Na lactate-3-^{14}C, 5 mM; and 200 mg tissue. The substrate was introduced into the Warburg flasks immediately before starting the incubation. For purposes of comparison in this investigation the same standard incubation conditions were used with all tissues. Preliminary experiments have shown that the incubation mixture used by Brin et al. (1952) in comparative studies on lactate oxidation gave consistently more active preparations than other media investigated.

Results — The oxidation of lactate to CO_2 by trout tissues was determined with lactate-1-^{14}C or lactate-3-^{14}C as substrate using an incubation time ranging from 30 min to 3 hr at 15 C. The following tissues were examined: dorsal white muscle, red lateral line muscle, heart, liver, kidney, and gills. For comparison, the results are presented jointly in Fig. 1A for lactate-1-^{14}C and in Fig. 1B for lactate-3-^{14}C. With all the tissues tested, the formation of $^{14}CO_2$ from labelled lactate was considerably higher for lactate-1-^{14}C than for lactate-3-^{14}C, reaching, respectively, 16.90% and 3.35% conversion for the most active tissues at the end of 3 hr incubation. With lactate-1-^{14}C, liver showed the highest activity and white muscle the lowest. For remaining tissues, kidney had the highest activity, followed by gills, red muscle, and heart, respectively. With lactate-3-^{14}C as substrate, a different spectrum of activities was observed: the white muscle still showed the lowest activity, but gills showed the highest activity, followed by kidney, red muscle, liver, and heart.

In Table 1, the values obtained for each tissue at the end of 3 hr incubation are expressed as specific activity on molar basis and the ratio between $^{14}CO_2$ formation from C-1 and C-3 of lactate is also indicated. It is apparent that the liver differs from the other tissues by showing a much higher value for this ratio. This suggests that in liver a comparatively smaller part of lactate, undergoing the initial decarboxylation, is subsequently oxidized completely.

The effect of various cofactors on the oxidation of lactate was determined with red muscle and liver (Table 2). Both tissues showed essentially similar response. Omission of Mg^{++} (5 mM) had no significant effect, whereas the addition of the oxidized form of diphosphopyridine nucleotide (NAD) (0.15 mM) strongly stimulated the oxidation of both substrates. Cocarboxylates (0.20 mM) had no effect on $^{14}CO_2$ production from lactate-1-^{14}C nor did coenzyme A (0.10 mM) on that liberated from lactate-3-^{14}C.

Discussion — Lactate labelled specifically in C-1 or C-3 was used in the present study to distinguish between two different stages in the oxidative metabolism. The existing evidence suggests that the general mechanism of lactate oxidation in fish does not differ from that established in mammalian tissues (Hochachka 1969). According to the main pathway of lactate oxidation in animal tissue, the liberation of $^{14}CO_2$ from lactate-1-^{14}C results from the conversion of lactate to pyruvate, followed by the oxidative decarboxylation of the latter. After being converted to acetyl-coenzyme A the remaining two carbons of lactate may undergo a complete oxidation from the action of the enzymes of the tricarboxylic acid cycle. This oxidative process is reflected by the liberation of $^{14}CO_2$ from lactate-3-^{14}C. A different physiological significance must be attached to these two stages in lactate oxidation. The release of $^{14}CO_2$ from lactate-3-^{14}C indicates that the tissue has the necessary enzyme system for supplying the energy through oxidation of lactate, since the tricarboxylic acid cycle implicated in the process is known to be the main energy yielding pathway of the oxidative metabolism. The formation of $^{14}CO_2$ from lactate-1-^{14}C reflects the ability of the tissue to metabolise lactate and pyruvate and it implies the formation of acetyl-coenzyme A, which may undergo a further oxidation or be involved in the biosynthesis of fatty acids and other tissue constituents.

Our results, showing a considerably higher yield of $^{14}CO_2$ from lactate-1-^{14}C than from lactate-3-^{14}C, are consistent with the idea that the two carbon fragment remaining after the oxidative decarboxylation of pyruvate, rather than being completely oxidized, is partially diverted to biosynthetic pathways. It is also possible that the lower yield of $^{14}CO_2$ from lactate-3-^{14}C is partially due to dilution of the two carbon fragment as it recycles in the pool of intermediates involved in the tricarboxylic acid cycle. It

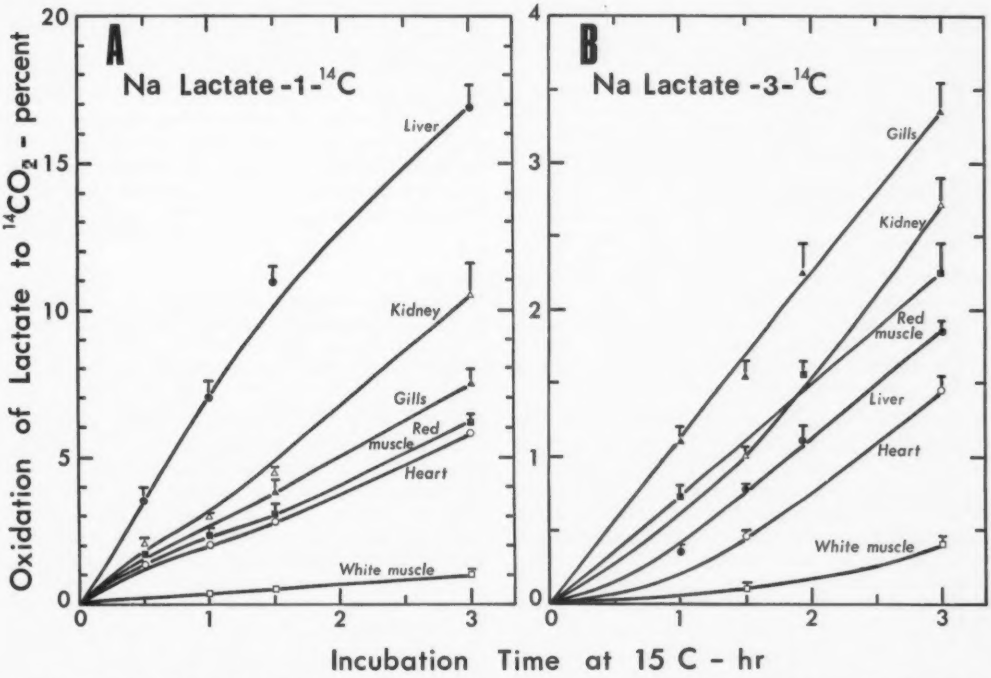

FIG. 1. Effect of the incubation time on the oxidation of lactate to CO_2 by rainbow trout tissues. For incubation conditions, see *Material and methods*. Each point represents the mean value from three incubations, the standard error is indicated by a vertical line.

TABLE 1. Oxidation of lactate to CO_2. Specific activity of rainbow trout tissues and ratio between $^{14}CO_2$ formation from -1-^{14}C and -3-^{14}C lactate.

Tissue	Specific activity[a]		Ratio between $^{14}CO_2$ formation
	Na-lactate-1-^{14}C	Na-lactate-3-^{14}C	Na-lactate-1-^{14}C / Na-lactate-3-^{14}C
Liver	2805±141[b]	309±12	9.07
Kidney	1743±186	450±30	3.87
Gills	1245±83	556±32	2.23
Red muscle	1029±50	374±32	2.75
Heart	963±16	241±15	3.99
White muscle	166±25	68±10	2.44

[a] mμmoles substrate converted to $^{14}CO_2$/g wet tissue/hr at 15 C. Standard incubation medium, without $MgCl_2$, see *Material and methods*, Incubation time–3 hr.

[b] Mean value ± standard error from three incubations.

TABLE 2. Effect of additives on oxidation of lactate-1-^{14}C and lactate-3-^{14}C by red lateral line muscle and liver from rainbow trout.

Additives		Na-lactate-1-^{14}C		Na-lactate-3-^{14}C	
		Red muscle	Liver	Red muscle	liver
Control[a]		100.00±4.20	100.00±6.78	100.00±10.27	100.00±2.33
$MgCl_2$	5.00 mM	90.50±2.87	106.95±0.92	94.40±8.13	89.83±5.27
$MgCl_2$ NAD	5.00 mM 0.15 mM	152.73±5.23[b,c]	166.10±5.38[c]	181.13±20.50[c]	135.07±10.21[c]
$MgCl_2$ Cocarboxylase	5.00 mM 0.20 mM	87.93±4.36	112.97±2.25	–	–
$MgCl_2$ NAD Cocarboxylase	5.00 mM 0.15 mM 0.20 mM	142.33±10.22[c]	171.33±7.95[c]	–	–
$MgCl_2$ NAD Coenzyme A	5.00 mM 0.15 mM 0.10 mM	–	–	178.20±7.83	131.64±2.21[c]

[a] Standard incubation medium, without $MgCl_2$, see *Material and methods*. Incubation for 60 min at 15 C.

[b] Mean value ± standard error from three incubations. The activity is expressed in terms of that of the control, which is taken as equal to 100.

[c] Indicates that there is a statistically significant difference between the treatment and the control (*t*-test).

is noteworthy that Blazka (1958) found that, in carp (*Cyprinus carpio*) maintained for a prolonged period under anoxic conditions, lactate did not accumulate, but there was a significant formation of fat. Under severe hypoxia Heath and Pritchard (1965) observed an accumulation of lactate in bluegill sunfish (*Lepomis macrochirus*) and cutthroat (*Salmo clarki*). The data, showing that the formation of $^{14}CO_2$ from lactate-1-^{14}C is promoted by liver to a much higher extent than by other tissues, suggest that, in trout, liver plays a significant role in the catabolism of lactate. As far as the complete oxidation of lactate is concerned, the activity in liver remains below that found in gills, kidney, and red muscle. This appears to indicate that in liver C-2 and C-3 of lactate are used to a larger degree for biosynthetic processes. It was surprising to find that gills show a comparatively high ability to promote the complete oxidation of lactate. Since the gills are well provided with blood stream carrying lactate, it appears likely that energy required for exchange reactions of gill filaments is partially supplied through lactate oxidation. The high capacity of gills for the oxidative metabolism of lactate is consistent with the reported observations made by electron microscopy on their ultrastructure, which show that in gill filaments of teleost fish the salt secretory epithelium is composed of cells possessing a very dense population of mitochondria (Conte 1969 and references cited). The significant oxidative activity shown by the red lateral line muscle, heart, and kidney is in agreement with the evidence presented earlier, which indicated the ability of these tissues to oxidize acetate and fatty acids (Bilinski 1969 and references cited; Bilinski and Jonas 1970). The poor ability of the white muscle to oxidize lactate reflects well the fact that in this type of muscular tissue the energy is supplied primarily by anaerobic glycolysis. Lactate dehydrogenase is known to exist in the white muscle of fish and other animal species in a molecular form specially adapted for the conversion to lactate of the large amounts of pyruvate formed by glycolysis (Dawson et al. 1964). The data showing the pronounced effect of NAD on the oxidative activity in trout liver and red muscle are consistent with the key role played by lactate dehydrogenase in regulating lactate metabolism.

The results of the present study, indicating that several tissues of rainbow trout are well provided with the enzyme system required for the oxidation of lactate, agree with the supposition made in several studies on lactate metabolism in fish in vivo. In experiments conducted with rainbow trout during and following exercise, Black et al. (1966) found that there was no evidence that glycogen is being deposited in the liver during the recovery period in which lactate is being removed from the blood stream. Since muscle glycogen was not restored to its initial level for a considerable period of time, Black et al. (1966) inferred that part of the circulating lactate may have been oxidized. In a study conducted with cod, plaice, and bass; Dando (1969) also suggested that the lactate produced in the white muscle is probably reoxidized. From a study on the effects of physical exertion on glycogen and lactate concentrations in cod, Beamish (1968) inferred that lactic acid was being oxidized and he suggested that this process may be more important at the medium, rather than at the high swimming speeds when the oxygenation of the tissues cannot keep pace with the production of lactate. Nagai and Ikeda (1971) found that glucose-6-^{14}C, administered to carp in vivo, was scarcely incorporated into glycogen, but oxidized to $^{14}CO_2$. Using a direct electrical stimulation of the lateral musculature of carp, Wittenberger and Diaciuc (1965) concluded that the red muscle plays a key role in the oxidation of lactate formed in the adjacent white muscle. In a study conducted with Black Sea scad, Wittenberger (1968) found that muscular work leads to an intensification of glycolysis in the white muscle, and of oxygen consumption in the red muscle as well as in liver.

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Differences in Littoral Fauna Due to Fluctuating Water Levels Below a Hydroelectric Dam

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Fisher, S. G., and A. LaVoy. 1972. Differences in littoral fauna due to fluctuating water levels below a hydroelectric dam. J. Fish. Res. Bd. Canada 29: 1472–1476.

Water level fluctuations below a hydroelectric dam on the Connecticut River produce a freshwater "intertidal" zone. Along a transect in this zone from high to low water mark benthic invertebrates increased markedly in density and taxonomic diversity. Community composition shifted from chironomid–oligochaete predominance on the most exposed sites to mollusc predominance on the least exposed sites.

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Les fluctuations du niveau de l'eau en aval d'un barrage hydroélectrique dans la rivière Connecticut produisent une zone "intertidale" d'eau douce. La densité et la diversité des animaux benthiques augmentent notablement le long d'une coupe transversale entre les haut et bas niveaux dans cette zone. La prédominance chironomides–oligochètes des communautés les plus exposées fait place à celle des mollusques aux endroits les moins exposés.

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This note describes benthic macroinvertebrate communities on periodically exposed substrates below a hydroelectric dam on the Connecticut River in central Massachusetts.

Hydroelectric dams have transformed the Connecticut River from its original free-flowing state to a stair-step series of long narrow ponds. Hydroelectric power generation is often not continuous, but generally occurs only during hours of high power demand (1000–2000 hr). During daytime, water levels rise above dams and fall below. At night, sluice gates are closed, ponds fill, and the water level below dams drops. Fluctuating water levels are most pronounced during summer and early autumn months, when the natural flow of the river is low and no water at all may be released for up to 14 hr per week day and nearly 42 hr on weekends (U.S. Geological Survey discharge data).

Water level fluctuations of this sort are responsible for the periodic exposure of the littoral zone, producing a freshwater "intertidal" zone which is somewhat analogous to the marine "intertidal." The "intertidal" zone of rivers differs from its marine counterpart in that 1) the tidal period is irregular, but usually diel, 2) the medium is fresh rather than salt water, 3) degree of exposure is related to season, being most pronounced during summer, and 4) the zone is of recent origin, so that sufficient time has not elapsed to allow the evolution of a well-adapted indigenous fauna.

While some workers have studied the fauna of freshwater systems subjected to periodic drying, such as vernal ponds (Hoff 1943), intermittent streams (Moon 1956), and lacustrine shoreline zones subjected to periodic flooding (Moon 1935), none of these systems has tidal periods shorter than one month. In most cases, the period is annual.

Materials and methods — Our primary sampling site was a bar 425 m long and approximately 70 m wide located 10 km below the Turner's Falls dam in Montague, Mass. The bar is completely submerged during periods of high discharge and is exposed during low flow. Tidal amplitude is approximately 1.0 m at the bar and 2.0 m immediately below the dam. Substrate is a uniform mixture of sand and gravel, approximately equally divided by weight into 0–1, 1–5, and >5 cm diameter size classes. The organic content of the substrate (loss on ignition) is 0.2% by weight or about 3.8 g/m². Vascular plants are rare on the bar. Attached algae were not studied.

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A transect running from the high water mark past the low water mark was established and divided into four zones, designated 1–4, which were exposed 70, 40, 13, and 0% of the time in summer, respectively. Macroinvertebrates in each zone were sampled semi-monthly from July to mid-September, 1971, with a 500 cm^2 cylindrical metal sampler (Whitley 1962). The sampler was pushed 10 cm into the substrate and the sediment within the sampler was removed, then taken to the laboratory for sorting and analysis. One sample was taken at each site on each sampling date. Large molluscs were sampled separately by means of a series of ten 50 m^2 circular plots per zone.

All samples were sorted by elutriation (Lauff et al. 1968). Only those organisms retained on a 0.5-mm mesh screen were processed. Animals were identified to genus where possible, using standard keys (Ward and Whipple 1959, Pennak 1953). Standing crop data for five sampling dates were averaged to yield mean summer standing crops for each zone on the transect. Biomass (ash-free dry weight) of selected faunal categories was computed as the difference between oven dry weight (95 C for 24 hr) and weight of ash (550 C for 2 hr).

While only one transect was sampled in this study, the bar is very homogeneous in appearance and is similar to other bars in this section of the river. Selected quantitative samples taken at other sites on the bar were similar in composition to samples taken from our transect, which suggests that our transect is representative of the habitat which we purport to describe.

In order to determine the vertical distribution of organisms in the substrate, the fauna was also sampled by allowing buried metal cylinders (cans 17.5×10.5 cm) to become colonized over two 4-week periods (July–September). Cylinders were filled with substrate from zone 1 and were placed in the other zones in pairs. Top and bottom halves of the cans were sorted separately to determine the vertical distribution of the fauna and to evaluate the efficiency of our primary sampling method. Coleman and Hynes (1970) performed similar experiments on inundated substrates in the Speed River, Ont., and found no diminution of invertebrate numbers to a depth of 30 cm in the sediments. Our results, however, indicated that approximately 81% of the organisms on our transect were distributed in the upper 7.5 cm of sediment. The numbers per m^2 and the percentages in the upper 7.5 cm in the various zones were:

Zone	1	2	3	4	Total
Number/m^2	1689	1020	2243	9277	3557
Percent in upper 7.5 cm	94	71	66	91	81

Since we sampled to a depth of 10 cm, we feel we removed the bulk of organisms present at our sites.

Results and discussion — Our results clearly show that benthic invertebrate communities of periodically exposed areas were lower in density and diversity than communities in continuously flooded areas. Pronounced increases in diversity, biomass, numbers, and number of taxa occurred from zones 1–3 (Fig. 1). Zone 4, which was never exposed, was not significantly different from zone 3, which was exposed 13% of the time. This suggests that the benthic community may tolerate brief periods of exposure without significant change. The greatest discontinuity occurred between zones 3 and 2, where biomass was reduced by an order of magnitude (Table 1). Much of this change in biomass can be attributed to the intolerance of unionid molluscs to exposure.

The discontinuity between zones 2 and 3 can also be documented by changes in community composition (Table 2). With the exception of chironomids, insects were extremely rare in zones 1 and 2. Those insects which were present were probably washed onto the site during periods of inundation. *Amnicola*

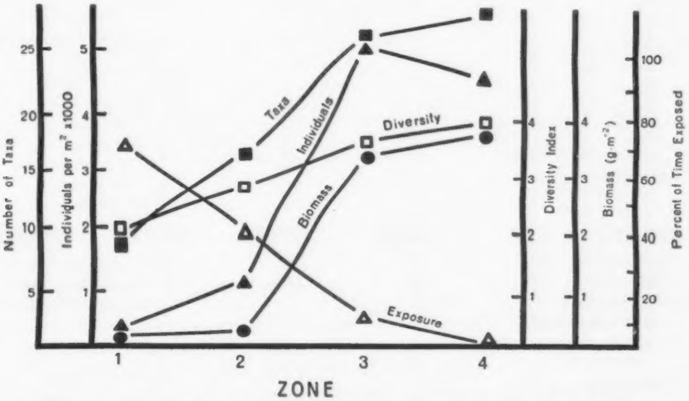

FIG. 1. Distribution of benthic macroinvertebrates along transect in the Connecticut River.

sp. was the only mollusc found in significant numbers in zones 1 and 2. In zones 3 and 4, molluscs predominated, comprising over 90% of the biomass and approximately 68% of the numbers present. *Lumbricus terrestris* was collected only in zones 1 and 2. Our transect, therefore, had characteristics of a terrestrial–aquatic continuum.

It is unlikely that stable, productive freshwater communities can become established in the periodically exposed biotope, the marine analogue of which is highly productive. Fluctuating water level ecosystems are often productive and attain a high degree of "pulse stability" provided that the community present is adapted to the frequency and magnitude of fluctuation present (Odum 1969). This degree of adaptation requires time measurable on the evolutionary time scale. Sufficient time has not been available for the evolution of complex communities suited to this freshwater intertidal biotope — a recent artifact of Man's activities.

Alteration of shallow water habitats is a cost which must be evaluated when assessing the environmental impact of water level manipulation

TABLE 1. Mean standing crops (Grams ash-free dry weight/m^2) of selected faunal categories along the Connecticut River transect. Values in lower rows are percentages of total biomasses in the various zones.

Taxon	Zone 1	2	3	4
Mollusca				
Amnicola sp.	–	0.14	2.0	1.3
	<1	36.7	56.1	35.2
Gyraulus sp.	0	0.10	0.15	0.07
	0	26.0	4.3	1.9
Lampsilis sp.	0	0	0.92	1.8
	0	0	26.4	49.1
Pisidium sp.	–	0.001	0.008	0.006
	<1	0.2	0.2	0.2
Ligumia sp.	0	0	0.15	0.25
	0	0	4.4	6.5
Total	–	0.24	3.2	3.4
	<1	62.9	91.4	92.9
All other taxa	0.11	0.14	0.30	0.26
	99	37.1	8.6	7.1
Total biomass (g/m^2)	0.11	0.38	3.5	3.7

TABLE 2. Check list and numbers/m^2 of "intertidal" fauna along transect. Each number in parentheses indicates the percentage of the total community in each zone represented bk the given taxon.

Taxon	Zone[a] 1	2	3	4
Platyhelminthes				
Dugesia sp.	0	0	44(0.8)	76(1.6)
Rhabdocoela[b]				
Nematoda	26(6.7)	376(30)	56(1)	84(1.8)
Sp. 1	13	340	28	60
Sp. 2	13	36	28	24
Annelida	207(54)	36(2.8)	309(5.9)	482(10.4)
Oligochaeta				
Sp. 1	7	16	112	68
Sp. 2	187	4	172	324
Sp. 3	0	0	20	48
Lumbricus terrestris	13	16	0	0
Hirudinea				
Helobdella sp.	0	0	5	12
Arthropoda	134(35)	600(47)	980(19)	1124(24.2)
Hydracarina	0	0	52	12
Cladocera	0	0	4	4
Amphipoda				
Hyallela azteca[b]				
Odonata				
Gomphus sp.	0	0	4	0
Coleoptera				
Anchycteis sp.	0	4	8	20
Agabus sp.	0	4	0	0

(*Continued*)

TABLE 2. Check list and numbers/m² of "intertidal" fauna along transect. Each number in parentheses indicates the percentage of the total community in each zone represented by the given taxon. — (*Concluded*)

Taxon	Zone[a]			
	1	2	3	4
Neuroptera				
Climacia areolaris[b]				
Ephemeroptera				
Stenonema sp.	0	0	0	12
Ephemerella sp.	0	0	20	24
Tricorythodes sp.	7	0	76	156
Caenis sp.	0	0	12	4
Paraleptophlebia sp.[b]				
Ephoron sp.	0	0	0	4
Trichoptera				
Limnephilus sp.	0	4	4	20
Molanna sp.	0	0	0	4
Hydropsyche sp.[b]				
Lepidostoma sp.	0	0	0	4
Cheumatopsyche sp.	0	0	12	48
Tascobia sp.	0	0	4	0
Orthotrichia sp.	0	0	4	4
Unidentified pupae	0	0	16	16
Rhyacophila sp.[b]				
Diptera				
Tipulidae				
Erioptera sp.	0	4	0	0
Pedicia sp.	0	8	0	0
Helius sp.	0	8	0	0
Antocha sp.	0	12	0	0
Chironomidae	127	556	764	792
Simuliidae[b]				
Mollusca	20(5.2)	256(20)	3884(74)	2880(62)
Gastropoda				
Physa sp.	0	8	4	12
Gyraulus sp.	0	4	52	28
Ferrissia sp.	0	0	220	228
Amnicola sp.	13	240	3520	2524
Pelycypoda				
Sphaeridae				
Pisidium sp.	7	4	52	36
Sphaerium sp.[b]				
Musculium sp.[b]				
Unionidae				
Lampsilis sp.	0	0	32	52
Ligumia sp.	0	0	0.23	0.37
Anodonta sp.	0	0	4	0
Elliptio sp.[b]				
All taxa	387	1268	5273	4646
Total taxa present	9	17	27	29
Total individuals[c]	58	318	1318	1168
Diversity index[d]	1.97	2.78	3.62	3.96

[a] Percent exposure times by zone: 1, 70%; 2, 41%; 3, 13%; 4, 0%.

[b] Taxa present but not collected in quantitative samples.

[c] Absolute number of individuals collected (for diversity computations).

[d] Taxonomic diversity index (D) = $(S-1)/\log_e N$, where S = number of taxa present and N = number of individuals.

programs. The total cost must of course be assessed in terms of the entire river ecosystem. Our study treated only a portion of the system — the benthic invertebrates of exposed areas. The significance of this effect on the whole ecosystem is a function of the total area exposed, which in turn depends upon channel morphometry. While we do not know the area of the Connecticut River which is periodically exposed, approximately half of the 400 linear miles of the river is subjected to periodic drawdown. Effects of water level fluctuations should also be assessed in terms of primary and secondary productivity, fish migration and spawning behavior, sedimentation rates, waste assimilation capacity, and other whole system properties.

The problem of periodic exposure could be partially alleviated by low flow augmentation — the storage of spring runoff and its subsequent release during periods of low discharge. This remedy, however, trades main stem littoral stability for instability elsewhere, e.g. tributary reservoirs. Furthermore, restoration of mean historical discharge rates is effected at the expense of the whole riverine ecosystem (Brower 1971). Finally, while water level fluctuations induced by main stem hydroelectric generation can be minimized by a modified program of low flow augmentation, the problem will persist and, in fact, intensify, if pumped storage systems proliferate in the drainage basin.

In summary, our data clearly show that water level fluctuations resulting from conventional hydroelectric power generation may prevent the establishment of normal benthic invertebrate communities on periodically exposed areas. The total environmental cost of this practice should, however, be assessed in the context of the entire riverine ecosystem.

Acknowledgments — We thank the United States Geological Survey, Water Resources Division, for providing the discharge data used in this study. Professor I. Sprague verified the insect identifications. This work was supported in part by the Ina Stillman Stryker Fellowship at Mount Holyoke College.

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Sight Records of Right Whales (*Eubalaena glacialis*) and Finback Whales (*Balaenoptera physalus*) from the Lower Bay of Fundy

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ARNOLD, P. W., AND D. E. GASKIN. 1972. Sight records of right whales (*Eubalaena glacialis*) and finback whales (*Balaenoptera physalus*) from the lower Bay of Fundy. J. Fish. Res. Bd. Canada 29: 1477–1478.

At least five right whales (*Eubalaena glacialis*) were observed by the authors in the lower Bay of Fundy between August 22–31, 1971. Some limited notes on behavior and movements are recorded.

ARNOLD, P. W., AND D. E. GASKIN. 1972. Sight records of right whales (*Eubalaena glacialis*) and finback whales (*Balaenoptera physalus*) from the lower Bay of Fundy. J. Fish. Res. Bd. Canada 29: 1477–1478.

Les auteurs ont observé au moins cinq baleines franches, (*Eubalaena glacialis*) à l'entrée de la baie de Fundy, du 22 au 31 août 1971. Ils enregistrent quelques observations sommaires sur leur comportement et leurs déplacements.

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NEAVE and Wright (1968) included in their compilation of cetacean sightings from the lower Bay of Fundy a record of 15 right whales (*Eubalaena glacialis*) seen during August. Schevill (1968) strongly criticized the methodology of these authors and considered their sight record "unconfirmed."

During an ecological study of the harbor porpoise, *Phocoena phocoena*, a team of trained observers has carried out extensive observations in the lower Bay of Fundy, centered on the mouth of Passamaquoddy Bay, N.B. (Fig. 1), from May to September in each of the years 1969–71.

RIGHT WHALE SIGHTINGS

On August 22, 1971, we sighted a large whale which brought its flukes clear of the water when diving deeply. This was subsequently identified as a right whale by its strongly arched upper jaw with characteristic "bonnet" of lightened, rough, epidermal outgrowths; V-shaped spout; absence of dorsal fin; and distinctive tapered flukes with smooth posterior margin. The animal lay quietly or moved slowly forward when at the surface, breathing regularly. Long dives were preceded by a shallow roll, followed immediately by a more pronounced roll in which initially up to one-third of the head was brought clear of the water, and the tail, with flukes, was exposed in the final part of the sequence. On only three occasions was the respiratory rate timed; the whales took 8–10 breaths, and then submerged for a period of 10–12 min. The sighting was made in an area with water depths of 60–100 m.

On August 26 at 1850 hr a single right whale was seen breaching eight times in succession. On one occasion the whale left the water entirely; its proportionately large triangular flippers were held at right angles to the long axis of the body. The large flippers and deep body contrasted sharply with the relatively small flippers and elongate cigar-shaped form of a finback (*Balaenoptera physalus*) which we observed breach twice in succession on August 18. Finbacks are not uncommon in our study area in late summer, but this was the only time we observed breaching behavior.

On August 29 we recorded no less than five right whales in the Deer Island area. One was solitary, while the other four formed a loose school covering a quarter square mile area. One of the four was a large calf (5m, estimated). On several occasions one of the large whales lay on its side with one fluke and one flipper out of water. Once it appeared that this animal was nursing the calf, but another lone whale was seen to adopt the same posture. Shortly after, we noted two right whales raise their flukes and submerge in unison, their bodies closely apposed. We were often able to observe these animals from less than 30 m, though they became more wary of the boat as the period of observation increased. Several color photographs and about 15 m

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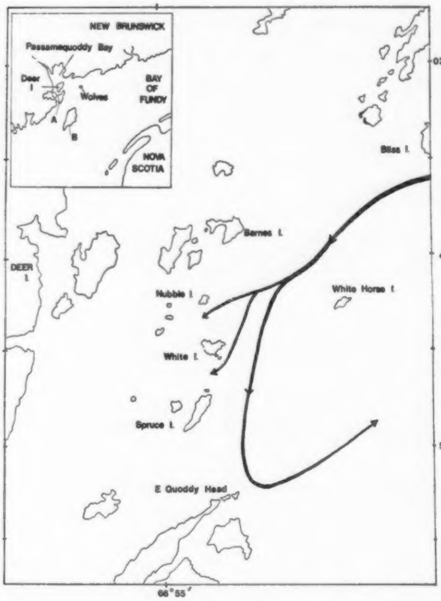

FIG. 1. Detail of Western Isles, at mouth of Passamaquoddy Bay, N.B., where right whales (*Eubalaena glacialis*) were sighted in August, 1971. Arrows show routes observed to be followed by finback whales (*Balaenoptera physalus*) each day during the same month. Inset shows lower Bay of Fundy: A, Campobello Island; B, Grand Manan Island.

of 8 mm movie film were taken. While these serve to confirm identification, the quality is not sufficient to merit reproduction here. Besides, there are already excellent published photographs of right whales (see Caldwell and Caldwell 1972; Gaskin 1972).

One right whale in this group had a conspicuous spade-shaped outgrowth projecting posteriorly from the tip of the tail within the median notch of the flukes. This should act as a reliable mark for future encounters.

All but one of the right whale sightings recorded were in an area bounded by East Quoddy Head (Campobello Island), White Horse Island, and Barnes Island (Fig. 1), and all sightings but one were made on the ebb tide, the exception being a sighting $2\frac{3}{4}$ hr after low water. The single "offshore" sighting, near the Wolves (45°00′N, 66°43′W, approx.), was also on the early ebb. The right whales remained in the Deer Island area until the 2nd week of September (Mr A. MacKay personal communication) and shortly after this they were reported by local fishermen to have moved off Grand Manan Island. After August 31, pressure of other work prevented further detailed observations on our part.

FINBACK WHALE SIGHTINGS

Finback whales were observed from July 22 until August 31; from August 22 there were 6–10 of this species in the area. The finbacks appeared to follow a route on the flood tide from the northeast, past Bliss and White Horse islands to the channels between the inner islands (e.g. White and Nubble). Here they were frequently seen, occasionally surfacing on their sides, apparently feeding. Large numbers of euphausids were noted in these channels; the few specimens examined were *Meganyctiphanes norvegica*. Although apparently present from at least July 16 to August 22, 1971, a single minke whale, *Balaenoptera acutorostrata* (6 m, estimated), was observed too infrequently for any behavior pattern to be discerned. As with the other species, the assumption is made that the whales are not extraordinarily abundant in the region, but that the same individual was seen again and again.

While finbacks were also recorded in the study area in the summers 1969–70 and a minke whale in 1970, we did not see right whales till 1971. However, some Deer Island residents have apparently seen the species before but called it "humpback". Continued observations by trained observers are necessary to determine whether right whales regularly return to the Bay of Fundy or are of sporadic occurrence there.

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Some Life History Aspects of the Rock Crab, *Cancer irroratus*, in the Gulf of Maine[1]

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KROUSE, J. S. 1972. Some life history aspects of the rock crab, *Cancer irroratus*, in the Gulf of Maine. J. Fish. Res. Bd. Canada 29: 1479–1482.

Rock crabs, *Cancer irroratus*, were caught in wire lobster traps from 1968 through 1971 at Boothbay Harbor and in 1969 at Casco Bay, Maine. Females dominated the annual catches (except in Casco Bay) and width classes from 61 to 90 mm; while males were predominant above this size range. Rock crabs from Casco Bay were heavier at a given width than those from Boothbay Harbor. Soft-shelled females were caught mostly in the fall, while soft-shelled males appeared most frequently in late winter and early spring. The occurrence of newly berried females suggested that spawning (egg extrusion) took place in late fall and early winter, and hatching occurred in spring. Most female crabs attained sexual maturity between 70–80 mm carapace width, but a few matured at widths less than 70 mm.

KROUSE, J. S. 1972. Some life history aspects of the rock crab, *Cancer irroratus*, in the Gulf of Maine. J. Fish. Res. Bd. Canada 29: 1479–1482.

On a capturé des crabes communs, *Cancer irroratus*, dans des casiers métalliques à homards à Boothbay Harbour de 1968 à 1971 et dans la baie Casco en 1969. Les femelles prédominent dans les prises annuelles (sauf dans la baie Casco) et dans les classes de largeur de carapace de 61 à 90 mm; au-delà de cet intervalle, les mâles sont plus abondants. Pour une largeur donnée, les crabes de la baie Casco sont plus lourds que ceux de Boothbay Harbour. Les femelles à carapace molle sont capturées surtout en automne; les mâles dans cette condition se rencontrent plus fréquemment à la fin de l'hiver et au début du printemps. La présence de femelles nouvellement oeuvées suggère que la fraie (libération des oeufs) a lieu à la fin de l'automne et au début de l'hiver, et l'éclosion au printemps. La plupart des femelles atteignent la maturité sexuelle à une largeur de carapace d'environ 70 à 80 mm, bien que quelques-unes atteignent ce stade à des largeurs inférieures à 70 mm.

Received March 14, 1972

ALONG the Maine coast, the abundant rock crab (*Cancer irroratus*) supports a small fishery. The 1970 catch was only 1,571,140 lb, valued at $89,651. Fishing is primarily incidental to the lobster fishery.

This study was undertaken because of the likelihood of future expansion of the crab fishery and the scarcity of information on the species. This investigation, which has utilized data collected incidentally to the Lobster Research Program of the Maine Department of Sea and Shore Fisheries, is concerned with: (1) size composition and sex ratio of annual catches; (2) seasonal occurrence and size of ovigerous females; (3) incidence of molting; and (4) width–weight relations.

Methods and materials — Rock crabs were collected with rectangular vinyl-coated wire lobster traps (1 × 1 and 1 × 2 inch mesh) in coastal waters of Maine near Boothbay Harbor from May 1968 through December 1971, and in Casco Bay near Mere Point during May and July 1969. Most sampling was conducted on mud substrates interspersed with rock outcroppings in depths ranging from 15 to 60 ft.

Upon capture, each of the 7174 crabs was sexed and measured prior to its return to the sea. Carapace widths measured between the two most posterior notches on the anterolateral border were recorded to the nearest millimeter. Crabs were classified as newly molted if ventral surfaces of carapace and/or the proximal sections of the walking legs felt soft or spongy. Female crabs in the berried condition, or with empty egg cases attached to the swimmerets (indicating recent hatching), were also noted.

Width–weight relations were based on 272 crabs (145 males and 127 females) taken in Casco Bay in July 1969 and 168 crabs (47 males and 121 females) collected near Boothbay Harbor in July–August 1969. Wet weights were recorded to the nearest 10 g. The regression of weight on width was fitted by the method of least squares

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[1] This study was conducted in cooperation with the Department of Commerce, National Marine Fisheries Service, under Public Law 88–309, as amended, Commercial Fisheries Research and Development Act, Project 3-14-R.

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using the logarithmic transformation $\log_{10}W = \log_{10}a + b \log_{10}L$. An analysis of covariance was employed to determine whether or not the regression coefficients of males and females were significantly different.

Size composition — Since the size composition of annual catches from Boothbay Harbor did not vary year to year, catch data were combined from 1968–71. Width-frequency histograms clearly revealed the marked size disparity between males (generally larger) and females (Fig. 1). Phillips (1939) concluded that mature female *Cancer* crabs from the Pacific coast are usually smaller than mature males. Males from Casco Bay (mean 107 mm) were larger than males from Boothbay Harbor (mean 92 mm). The effects of gear selectivity are manifested in the histograms by: (1) the progressive decline in numbers of small crabs, and (2) the pronounced modes which denote size where crabs are fully vulnerable to the gear. Although these conspicuous modes occurred at smaller sizes for females than males, it seems unreasonable to assume that males would become fully vulnerable to the gear at a larger size than females. I attributed this dissimilarity in the size distribution to smaller males being unavailable to the gear. Small males (less than 90 mm carapace width) may concentrate themselves in shallower or deeper water than that sampled.

Sex ratio — There were more females than males in the Boothbay Harbor catch, 1968–71; conversely, there were fewer females than males in the 1969 catch from Casco Bay (Table 1). In both areas, females dominated the size classes between 61 and 90 mm. For carapace widths greater than 90 mm, males outnumbered females.

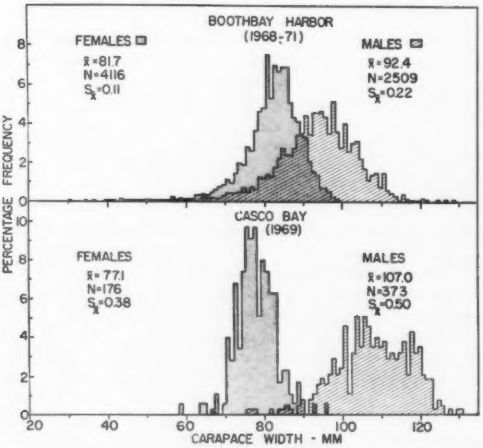

FIG. 1. Width–frequency distributions of rock crabs collected at Boothbay Harbor (1968–71) and Casco Bay (1969).

TABLE 1. Total number of rock crabs and percent females by size class for Casco Bay 1969 and Boothbay Harbor 1968–71.

Carapace width (*mm*)	Boothbay Harbor		Casco Bay	
	Total no.	Females (%)	Total no.	Females (%)
21–30	1	100	–	–
31–40	3	33.3	–	–
41–50	17	35.3	–	–
51–60	61	60.7	1	100
61–70	273	81.3	13	92.3
71–80	1531	87.5	125	97.6
81–90	2878	66.0	50	78.0
91–100	1335	22.6	81	2.5
101–110	476	1.5	139	0
111–120	53	0	117	0
121–130	4	0	23	0
Total	6632	62.1	549	32.1

Disparities in the overall sex ratios may be explained by: (1) the spatial separation of males smaller than about 90 mm carapace width from the segment of the population available to the gear; (2) differences in sex ratios between sampling sites (a cursory analysis indicates differences in sex ratios between sampling stations as well as seasonal changes within sites); and (3) possible differences in mortality rates (fishing mortality is greater for males since they attain larger sizes while most females never reach a harvestable size). Fluctuations in the sex ratio with size may also be assigned to the unavailability of small male crabs and to a retardation or cessation in the growth rate for females after the onset of sexual maturity. The female Dungeness crab, *Cancer magister*, of the Pacific coast has been observed by Cleaver (1944) to slow down its growth rate with the onset of maturity, while members of the spider crab family are known to terminate molting at maturity.

Maturity — A relative index of size at first maturity, time of spawning, and egg hatching was based upon the occurrence of egg bearing and egged-off (eggs have hatched but egg cases still cling to the swimmerets) females in the monthly samples. Berried females (width ranged from 62 to 99 mm) appeared most frequently from February through May with a gradual decline to August and then a marked reappearance in November and December

(Table 2). Egged-off females (width ranged from 55 to 96 mm) were most abundant from June through August with a conspicuous decline in the following months (Table 2).

These periodical appearances of berried and egged-off females indicate that egg extrusion occurs in late fall and winter from which time the eggs are carried externally until hatched the following spring. This is supported further by the observation of newly spawned orange eggs in late fall-early winter, followed by the more developed greyish-black eggs in late winter and spring. Cleaver (1944) noted that the Dungeness crab spawned in the late fall and the eggs were hatched in the spring.

TABLE 2. Total number of female rock crabs with the monthly percentage of berried and egged-off females collected at Boothbay Harbor from 1968–71 and July 1970–71, respectively.

	Berried		Egged-off	
Month	Total no.	(%) of catch	Total no.	(%) of catch
Jan.	0	0	–[a]	–
Feb.	35	20.0	–	–
Mar.	182	13.2	34	0
Apr.	53	13.2	–	–
May	116	21.6	–	–
June	500	7.8	88	19.3
July	824	2.1	582	30.8
Aug.	1581	0.7	631	14.9
Sept.	594	0	596	2.9
Oct.	309	0.6	80	1.3
Nov.	170	5.9	137	0.7
Dec.	92	5.4	31	0

[a] No samples taken.

TABLE 3. Percentage of soft-shelled crabs in monthly samples collected at Boothbay Harbor, 1969–71.

	Males		Females	
Month	Total no.	% shedders	Total no.	% shedders
Jan.	–[a]	–	–	–
Feb.	113	31.0	36	2.8
Mar.	110	29.1	68	2.9
Apr.	38	2.6	11	0
May	108	6.5	34	0
June	118	0.9	101	0
July	317	1.9	582	0.9
Aug.	552	1.6	1183	0.8
Sept.	198	0.5	616	3.4
Oct.	61	0	85	8.2
Nov.	37	2.7	23	0
Dec.	60	3.3	68	0

[a] No samples taken.

Molting — Information on molting was first collected in August 1969 (Table 3). The data indicate that months of peak shedding did not coincide for males and females. Soft males appeared most frequently during February and March and soft females in the fall.

Width–weight relation — The regression of total wet weight on carapace width was calculated for male and female rock crabs sampled at Casco Bay and Boothbay Harbor. The equation used was $W = aL^b$, where W = wet weight in grams, L = carapace width in millimeters, and a and b are constants.

Since analysis of covariance on the regression coefficients (Steel and Torrie 1960) indicated that

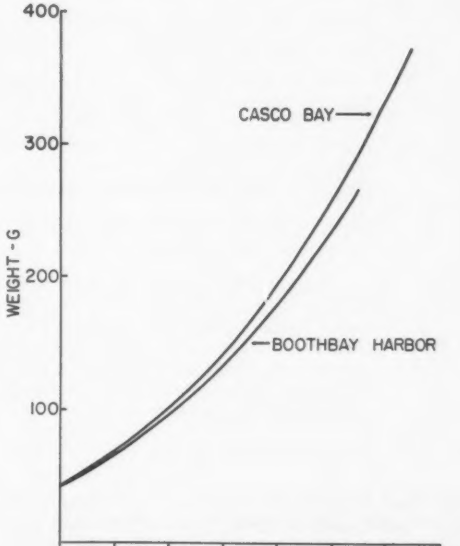

FIG. 2. Comparison of rock crab width–weight relations for sexes combined from Boothbay Harbor and Casco Bay. The curves represent weights calculated from the regression equations. The regression equations for Boothbay Harbor and Casco Bay are, respectively, $\log_{10} W = -3.39 + 2.82 \log_{10} L$ and $\log_{10} W = -3.60 + 2.94 \log_{10} L$.

width/weight ratios of males and females from the same area were not significantly different, sexes were combined by area. The regression coefficients (*a* and *b*) were:

Boothbay Harbor		Casco Bay	
a	*b*	*a*	*b*
–3.39	2.82	–3.60	2.94

Casco Bay rock crabs were heavier at a given width, particularly at the larger sizes where males predominated, than Boothbay Harbor crabs (Fig. 2).

Acknowledgments — I am grateful to Messrs R. Hanley, G. Brackett, R. Nunan, S. Ham, and A. Dolloff for their assistance in field collections and data compilations. I would also like to thank Mr J. C. Thomas for his suggestions and review of this manuscript.

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Fatty Acids in Surface Particulate Matter From the North Atlantic

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SCHULTZ, D. M., AND J. G. QUINN. 1972. Fatty acids in surface particulate matter from the North Atlantic. J. Fish Res. Bd. Canada 29: 1482–1486.

The fatty acid composition of particulate matter from surface waters in the North Atlantic has been investigated. A high proportion is long-chain polyunsaturated acids, typical of a marine origin. The low relative abundance of iso and anteiso 15-carbon acids indicates little bacterial contribution to the particulate matter. This fatty acid distribution is in contrast to that found in estuarine particulate matter, which contains only trace amounts of the long-chain polyunsaturated acids and substantial quantities of branched chain acids.

SCHULTZ, D. M., AND J. G. QUINN. 1972. Fatty acids in surface particulate matter from the North Atlantic. J. Fish. Res. Bd. Canada 29: 1482–1486.

Nous avons mesuré la teneur en acides gras de la matière particulaire des eaux superficielles de l'Atlantique Nord. Cette matière est constituée en grande partie d'acides polyinsaturés à longue chaîne, caractéristique d'une origine marine. L'abondance relativement faible d'acides *iso* et *anteiso* 15 carbone indique qu'il y a peu d'apport bactérien à la matière particulaire. Cette répartition des acides gras diffère de celle observée dans la matière particulaire d'estuaires, qui ne contient que des traces d'acides polyinsaturés à longue chaîne et une grande quantité d'acides à chaîne ramifiée.

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THE lipid fraction of sea surface film samples has been investigated by several workers (Garrett 1967; Jarvis et al. 1967; Duce et al. 1972). In general, they found an enrichment of surface-active lipid materials, e.g. fatty acids and fatty alcohols, at the air-sea interface. However, fatty acids found in particulate matter from surface waters (20 m), have been reported only by Williams (1965), who indicated that a high percentage of many varied unsaturated fatty acids are present. A substantial portion of the fatty acid composition of phytoplankton and zooplankton consists of long-chain polyunsaturated acids (Ackman et al. 1968; Chuecas and Riley 1969; Culkin and Morris 1969, 1970).

On R/V *Trident* Cruise 102 from Reykjavik, Iceland, to Halifax, Nova Scotia (August, 1971), samples were taken at seven stations (Table 1) to determine the fatty acid composition of open-ocean surface particulate matter and to compare it with particulate matter in estuarine samples from Narragansett Bay, R.I. Few data have been published on the fatty acid composition of particulate matter,

TABLE 1. Sample station positions on R/V *Trident* Cruise 102 (August, 1971).

Cruise station #	Date collected	Position
2	8/ 3/71	61°10′N22°58′W
6	8/ 6/71	58°24′N24°36′W
10	8/10/71	55°28′N37°07′W
12	8/12/71	53°47′N42°51′W
13	8/13/71	50°55′N47°34′W
14	8/14/71	50°15′N48°29′W
32	8/22/71	44°25′N54°28′W

which is of importance as a food source (Wood et al. 1969; Odum and de la Cruz 1967; Newall 1965; and Heald 1971).

Materials and methods — Surface samples (taken at 20 cm depth) were collected in 20-liter polyethylene carboys (previously rinsed with conc. HNO_3 and distilled water) from a raft rowed to about 100 to 500 m upwind from the ship. These samples were filtered through Gelman type A glass-fiber filters (initial pore size approximately 0.3 μ). The filters had been ignited at 450 C for 4 hr and then rinsed with 10 ml 0.1 N HCl and 10 ml each distilled MeOH, $CHCl_3$, and MeOH to remove all traces of fatty acids. All solvents used were freshly distilled through a 30-cm glass distillation column (Widmer) prior to use, and all glassware was rinsed the same as the filters. Immediately before use, the filters were again rinsed with distilled $CHCl_3$ and MeOH. About 8 liters of sea water from each sample were immediately filtered on board ship; the filters were then placed into 25-ml culture tubes, sealed with teflon-lined screw caps, and stored at –20 C in the ship's freezer. The tubes and teflon-lined screw caps had been cleaned previously by treatment with 24 ml 0.5 N KOH/MeOH for 1 hr at 100 C, and by rinsing with acid and solvents as described above. The control samples consisted of the reagents and of a treated filter, and the results in Table 2 have been corrected for acids in this control. The sample acids were at least five times higher than the control, averaging 15 times higher, and the acids in the control consisted of 14:0, 15:0, 16:0, 16:1, 18:0, and 18:1[2]. The high amount of unique polyunsaturated acids in several of the samples indicated little contamination, if any, by the ship's activities.

The maximum length of time samples were stored at –20 C was one month. A control on samples stored up to 6 weeks at –20 C run prior to the cruise showed no evidence of autoxidation. All samples were analyzed at the same time, and the samples collected first and stored the longest (stations 2, 6, and 10) had the highest amount of polyunsaturated acids, indicating autoxidation was not occurring.

At the end of the cruise, the samples were transferred from the ship's freezer to the laboratory freezer. For laboratory analysis, the samples were taken from the freezer, 20 μg internal standard (17:0) added, followed by 2 ml 0.5 N KOH/MeOH, 8 ml MeOH, and 5 ml

TABLE 2. Fatty acid weight percentages of open-ocean and Narragansett Bay particulate matter.

	Station no.							
Fatty acid	2	6	10	12	13	14	32	Narragansett Bay
14:0[a]	14.4	18.5	20.4	25.4	13.4	15.9	23.4	14.9
15[b]	3.6	2.0	2.4	2.0	1.7	2.7	5.1	4.1
15:0	2.2	1.9	3.0	2.5	2.1	2.5	3.2	3.0
16:0	27.1	28.6	33.0	33.0	38.1	41.8	45.1	33.7
16:1	6.4	4.7	4.1	6.1	8.2	7.0	8.3	20.1
16:2	1.5	0.8	1.0	2.6	2.5	1.4	2.6	2.2
18:0	3.7	3.2	2.7	3.3	4.4	5.8	1.7	4.3
18:1	9.2	7.6	4.4	4.1	9.7	9.3	7.7	8.6
18:2	3.8	3.9	2.2	2.6	5.6	3.4	2.8	3.5
18:3	2.3	2.3	3.7	2.2	6.3	5.1	tr[c]	5.7
18:4	4.6	4.2	4.9	3.6	5.0	5.2	tr	tr
20:4	5.9	5.3	3.4	3.5	3.1	tr	ND[d]	ND
22:4	4.2	6.6	8.5	3.5	tr	tr	ND	ND
22:6	11.3	10.4	6.3	5.6	tr	tr	ND	ND
Total μg/l:	26.3	20.5	10.1	12.0	4.8	3.8	3.6	41.4

[a] All fatty acids are given by normal chain length: number of double bonds.

[b] Consists of undifferentiated species including anteiso and iso 15, and a very small amount of 14:1.

[c] tr = trace.

[d] ND = None detected.

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[2] All fatty acids are given by normal chain length: number of double bonds.

benzene. The samples were saponified in the same tubes as they were stored in. After addition of the solvents to the tube, the tubes were flushed with nitrogen and sealed with teflon-lined screw caps. The filters were broken up thoroughly by vigorous shaking before heating at 100 C for 30 min, with shaking every 10 min. Each sample was checked to insure the *p*H was 10 or greater at the end of the reaction and then acidified to *p*H 2.0 or less with 8–10 ml of 0.3 N HCl (previously extracted with $CHCl_3$ to remove lipid contaminants). This acidification is necessary in order to prevent preferential loss of unsaturated fatty acids salts, which occurs when basic solutions are extracted (Van Der Veen et al. 1968). The tubes were centrifuged, and the benzene layer transferred to a 50-ml pear-shaped flask. The aqueous methanol layer was extracted twice more with 5-ml portions of petroleum ether, and the organic extracts combined and removed under vacuum on a flash evaporator. The residues were transferred from the pear-shaped flasks into 12-ml centrifuge tubes with 1 ml MeOH and 1 ml benzene. One ml 14% BF_3/MeOH was added, the tube flushed with N_2, sealed with a teflon-lined screw cap, and heated at 100 C for 5 min. At this point the solution was cooled, 4 ml petroleum ether and 4 ml $CHCl_3$-extracted distilled water were added, and the methyl esters isolated by extracting a total of three times with 5-ml portions of petroleum ether. The combined organic extracts, in a 50-ml pear-shaped flask, were evaporated under vacuum. The methyl esters were separated and purified using preparative thin-layer chromatography (TLC) on 10 × 20 cm plates of 0.37 mm thickness Silica Gel G. The solvent system used was petroleum ether/ethyl ether/acetic acid (95/5/1) and the TLC plates had been predeveloped in $CHCl_3$/MeOH (1/1) to remove lipid contaminants. The methyl ester band was visualized by brief exposure to iodine vapors, scraped from the plate, and the esters extracted from the silicic acid (about 0.5 g) with three 10 ml portions of $CHCl_3$/MeOH (9/1). After the solvents were removed under vacuum on a flash evaporator, a small amount of CS_2 was added and the samples were analyzed by gas-liquid chromatography (GLC).

The instruments used for the analyses were Hewlett-Packard Models 5750 and 700 flame-ionization gas chromatographs. The former model was equipped with a polar column (15% stabilized DEGS on Gas Chrom P, 80/100 mesh) and the latter model a nonpolar column (2% Apiezon L on Anakrom Q, 90/100 mesh). The columns were 2.1 m by 3.2 mm outside diameter (2.2 mm inside diameter) stainless steel and were operated at 180 C (polar) and 210 C (nonpolar), with nitrogen carrier gas (flow of 35–50 ml/min at 40–50 PSIG inlet pressure). The areas of naturally occurring component peaks were compared to the area of the internal standard peak to quantitate the results. The areas were measured by multiplying height by width at half-peak height.

The estuarine samples were collected at flood tide from a station at the mouth of Bissel Cove, Narragansett Bay. The collection procedure, preparation, and analysis of these samples were identical to those from the North Atlantic. The bay samples were collected in glass containers, but work in this laboratory on fatty acids in particulate matter with both polyethylene and glass containers has given essentially the same results. This would indicate that the polyethylene container does not sorb significant amounts of particulate lipid material.

Quantitative results with National Heart Institute Fatty Acid Standard mixture D agreed with the stated composition data with a relative error of less than 5% for major components (> 10% of total mixture) and less than 10% for minor components (< 10% of total mixture) (Horning et al. 1964). The accuracy of gas chromatographic analyses determined by the method of Herb and Martin (1970) is indicated by a value of 97% or greater using the above standard mixture. In all cases, quantitation was effected using the DEGS column. The relative retention times and quantities of samples 2 and 6 were compared with those of standard methyl esters on both the polar and nonpolar columns. Comparison of relative retention times and quantities before and after hydrogenation served to tentatively identify the acids in sample 2.

The presence of 20:4 was indicated by hydrogenation and chromatography on Apiezon L. This suggested that this component was an unsaturated 20-carbon acid and, in addition, that the relative retention time of this acid corresponded to the relative retention time of authentic 20:4 in a polyunsaturated standard. The 22:6 coincided with a standard on both polar and nonpolar columns before and after hydrogenation. Based on the levels of 22:6, 20:5 would be expected, but was not detected. The reasons for the absence of 20:5, as well as the relatively high amounts of 22:4 in several of the samples, have not been established.

This procedure differs from that given by Williams (1965) in several aspects. First, the samples are saponified, the salts converted to acids, and the acids methylated using BF_3/MeOH. Secondly, the methyl esters are separated and purified by TLC. Finally, a polar and a nonpolar column, as well as hydrogenation, are used to tentatively identify the acids in some of the samples.

Results — The fatty acid composition of the particulate matter is given in Table 2. Values of total fatty acids (free and esterified) present in the particulate matter (per liter) ranged from 4 to 26 μg. These data are from single analyses. However, similar multiple analyses on estuarine particulate matter give an average relative standard deviation of 18% for the method used.

Discussion — Some of the fatty acids reported here and in Williams' work as derived from particulate organic matter may in fact be accounted for by dissolved fatty acids, since glass-fiber filters retain these acids (Quinn and Meyers 1971). This introduces an important consideration concerning the operational definition of "particulate organic matter," which (as used here) includes all organic material retained in or on the filters, such as living and dead plankton, detritus with its associated organisms, minerals combined with organic matter, organic colloids and macromolecules, and organic matter sorbed to any of the above or to the filter itself. A better term might be "retained organic matter," which would include all of the above material, rather than "particulate organic matter," which implies only a size fractionation of particles. However, since the latter term is widely used, and allows a valuable comparison of samples obtained using similar filters, we will continue to use it in this paper. For example, with glass-fiber filters, our values range from 4–26 μg/liter and are in good agreement with Williams' values of 3–30 μg/liter.

The fatty acid composition of particulate matter from estuarine and nearshore environments has, to the best of our knowledge, not been reported in the current literature. Based on the average of monthly analyses (January–December, 1971) of particulate matter samples from Narragansett Bay, a major qualitative and quantitative difference can be seen between the pelagic samples reported here and estuarine samples (Table 2). This difference seems to stem from the source of the fatty acids. In the pelagic samples, the weight percentages of the branched 15 fatty acids (anteiso and iso) are low (range 1.7–5.1, average 2.8%, sd 1.2%). Based on work of Blumer (1970) involving dissolved organic compounds in sea water, the low relative abundance of these odd chain acids (which are usually the major branched-chain acids) would indicate relatively little bacteria present. The estuarine samples, on the other hand, are relatively high in these acids (range 1.6–11.4, average 4.1%, SD 2.8%). Other workers (Stauffer and MacIntyre 1970) report that for dissolved fatty acids, the C_{15} acids are found in relatively small amounts in the ocean, but in higher concentrations in the estuary.

The nature of some of the fatty acids (long chain, polyunsaturated acids) from North Atlantic particulate matter indicates an origin from marine organisms. Conversely, these acids are present in only trace amounts in the estuarine samples. From most samples of Narragansett Bay particulate matter, these unsaturated acids (18:4 or greater) have not been detected, whereas the open ocean samples showed a range of 0–22 (average 11.1%) (Table 2). The pelagic particulate matter fatty acids appear therefore to be derived from marine plankton, rather than the detritus and micro-organisms which apparently comprise the bulk of estuarine particulate matter. Alternatively, there may be two entirely different plankton populations in these two different environments. Of the two explanations, the first seems to be the more realistic, since some polyunsaturated fatty acids are a probable component of all marine plankton populations.

The decreasing relative abundance of polyunsaturated fatty acids, as well as a decrease in total concentration from station number 2 to 32, is not easily explained. However, there are at least two possible explanations. The first involves the influence of phytoplankton blooms on our samples. Several of our stations (2–12) would appear to have been collected in or immediately after a phytoplankton bloom, to account for the fatty acid composition. However, the relatively high amounts of 14:0 (a major fatty acid component of phytoplankton) in all of the samples cannot be adequately explained at this time. The second explanation involves quantitative and qualitative distribution of psychrophilic organisms. The general trend in decreasing concentration of total acids is from north to south, and this trend could be accounted for by a parallel decrease in abundance of these organisms, which supposedly have a high amount of polyunsaturated acids (Brock 1970).

It is believed that particulate matter is an important nutritional source, both directly and indirectly, to fish and marine mammals. The fatty acids are being studied as a possible tracer of this food source through the food chain. However, a more probable tracer because of their greater chemical stability is that of various plant and animal isoprenoid and paraffinic hydrocarbons (e.g. pristane, Blumer et al. 1964, 1971; Avigan et al. 1967; Avigan and Blumer 1968), and work is being conducted in this laboratory toward this goal.

Acknowledgments

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Mercury Content of Spiny Dogfish (*Squalus acanthias*) in the Strait of Georgia, British Columbia

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FORRESTER, C. R., K. S. KETCHEN, AND C. C. WONG. 1972. Mercury content of spiny dogfish (*Squalus acanthias*) in the Strait of Georgia, British Columbia. J. Fish. Res. Bd. Canada 29: 1487–1490.

Total mercury content of *Squalus acanthias* sampled in the Strait of Georgia reached levels of 0.5 ppm at fish lengths of 72 and 77 cm for male and female fish, respectively. For any given length above 65 cm the mercury content was higher among males than females and higher in samples taken off the Fraser River Estuary than in other areas of the Strait. Levels of mercury reached 1.7 ppm in males (to 95 cm in total length) and almost 2.0 ppm in females (to 120 cm in total length).

FORRESTER, C. R., K. S. KETCHEN, AND C. C. WONG. 1972. Mercury content of spiny dogfish (*Squalus acanthias* in the Strait of Georgia, British Columbia. J. Fish. Res. Bd. Canada 29: 1487–1490.

La teneur en Hg total de *Squalus acanthias* capturé dans le détroit de Georgie atteint un niveau de 0.5 ppm à des longueurs de 72 cm pour les mâles et de 77 cm pour les femelles. A une longueur donnée au-delà de 65 cm, la teneur en Hg est plus élevée chez les mâles que chez les femelles, plus élevée également dans les échantillons provenant de l'estuaire du fleuve Fraser que dans toute autre région du détroit. Hg atteint des niveaux de 1.7 ppm chez les mâles (jusqu'à 95 cm de longueur totale) et presque 2.0 ppm chez les femelles (jusqu'à 120 cm de longueur totale).

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MERCURY concentrations in fish from waters off British Columbia became of vital concern in January, 1971. At that time a shipment of flesh from spiny dogfish (*Squalus acanthias*), captured in the Strait of Georgia and prepared for export for human consumption, was found to contain mercury levels in excess of 0.5 ppm and export was delayed (Anon. 1971). The incident prompted further testing of other marine products. The Pacific Biological Station at Nanaimo, B.C., undertook a dogfish sampling program in the Strait of Georgia to determine whether or not there was any systematic pattern of mercury content in these fish in the Strait.

Materials and methods — During May–June, 1971, dogfish were collected with a small-meshed otter trawl, longline gear (both bottom and floating types), and handlines in four areas of the Strait of Georgia (Fig. 1). These were: A, French Creek to Oyster River; B, Lund to Pender Harbour; C, Nanoose Bay to Swanson Channel; and D, Point Grey to the United States–Canadian Border.

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Before field sampling began, one large (108 cm) female dogfish was tested to determine whether the mercury content varied from one part of the body to another. Analysis for methylmercury was not made, but it is assumed, on the basis of other studies, to be a high fraction of the total mercury content (Zitko et al. 1971). Samples were taken from five equally spaced sections along the side of the dogfish. Progressing from head to tail the analyses gave readings of 1.04, 1.01, 1.04, 1.00, and 0.92 ppm. On the strength of these results it was concluded that one sample per fish would be sufficient. Particular care was taken to collect specimens from a fixed position on the body, namely, from the dorsal musculature between the first and second dorsal fins. A total of 685 dogfish were captured from which 206 flesh samples were taken (Table 1). In addition, sets of 0+ and 1+ intra-uterine embryos were obtained in the Lund–Pender Harbour and Nanoose Bay–Swanson Channel areas.[1] Individual samples were deep frozen in plastic bags until time of analysis.

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[1] The female dogfish has a gestation period of nearly 2 full years. 0+ and 1+ refer, respectively, to the first and second years of life in the uterus.

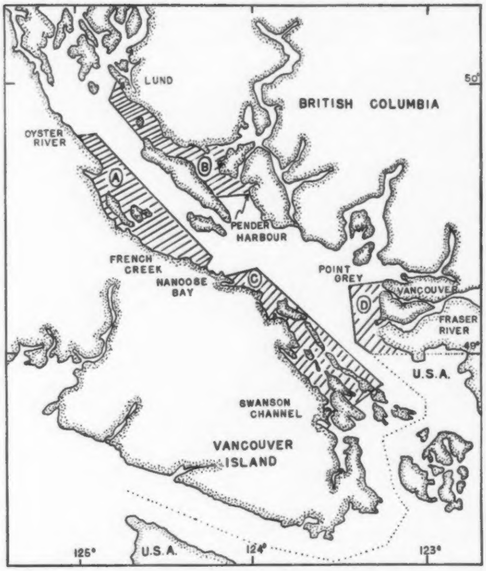

FIG. 1. Location of sampling areas (A, B, C, D) for *S. acanthias* in the Strait of Georgia.

TABLE 1. Size composition of juvenile and adult dogfish collected for mercury content analysis, by area and sex.

Size interval (*cm*)	Area A		Area B		Area C		Area D	
	♂	♀	♂	♀	♂	♀	♂	♀
<30	0	0	0	0	1	0	3	3
30–34	0	0	3	1	0	1	3	1
35–39	0	0	3	3	0	0	1	1
40–44	0	0	3	2	0	0	0	0
45–49	0	0	3	3	1	0	0	0
50–54	0	0	3	3	0	0	0	0
55–59	0	0	3	3	0	0	0	1
60–64	0	0	3	3	0	0	0	1
65–69	0	0	3	3	1	2	0	0
70–74	1	0	3	3	3	3	1	2
75–79	3	1	3	3	3	3	3	2
80–84	3	3	3	3	3	3	2	2
85–89	3	3	1	3	3	3	2	1
90–94	3	3	0	3	3	3	1	1
95–99	0	3	1	3	0	4	0	1
100–104	0	3	0	4	0	3	0	0
105–109	0	3	0	3	0	4	0	0
110–114	0	3	0	3	0	3	0	0
115–119	0	1	0	0	0	3	0	0
120–124	0	0	0	0	0	1	0	0
Total	13	23	35	49	18	36	16	16
Total	36		84		54		32	

Total mercury content (ppm wet weight) of the samples was determined through wet digestion and flameless atomic absorption spectrophotometry, according to the method described by Armstrong and Uthe (1971).

Results — The smallest and youngest dogfish sampled were intra-uterine embryos age 0+ and 1+ years. Age 0+ embryos were minute with a large yolk sac attached. Age 1+ embryos were approximately 15 cm in total length with smaller yolk sacs. Mercury content ranged from 0.01 to 0.05 ppm and there appeared to be no difference in content between age 0+ and 1+ embryos (Table 2). There appeared to be a higher mercury content in embryos collected in the Nanoose Bay-Swanson Channel area (actually, Booth Bay, Saltspring Island) than in embryos taken in the Lund–Pender Harbour region (actually, in Thunder Bay near the mouth of Jervis Inlet). The average mercury content was 0.029 ppm in the former and 0.015 ppm in the latter embryos. However, the sample sizes were too small to be tested statistically.

Juvenile and adult dogfish sampled ranged in total length from 25 to 95 cm for males, and 27 to 120 cm for females. Mercury content varied curvilinearly with body length (Fig. 2). Following are the formulae expressing this relation:

$$\text{Males: } y = (157 \times 10^{-9})x^{3.511}$$
$$\text{Females: } y = (186 \times 10^{-7})x^{2.347}$$

where y = mercury content (ppm) and x = body length (cm). Above a length of 65 cm mercury concentration appeared to be higher, for a given length, among males than among females, reaching the 0.5 ppm level in the former at about 72 cm (28.5 inches), in the latter at about 77 cm (30.5

TABLE 2. Mercury levels (*ppm*) in ovarian dogfish embryos, by age-groups, taken in May–June 1971, in the Strait of Georgia.

Area	Age-group 0+	Age-group 1+	Mean total
Lund–Pender Harbour	0.01 0.01 0.03	0.02 0.01 0.01	
Mean	0.017	0.013	0.015
Nanoose Bay–Swanson Channel	0.03 0.02 0.04	0.02 0.01 0.05	
Mean	0.030	0.027	0.029
Overall mean	0.023	0.020	0.022

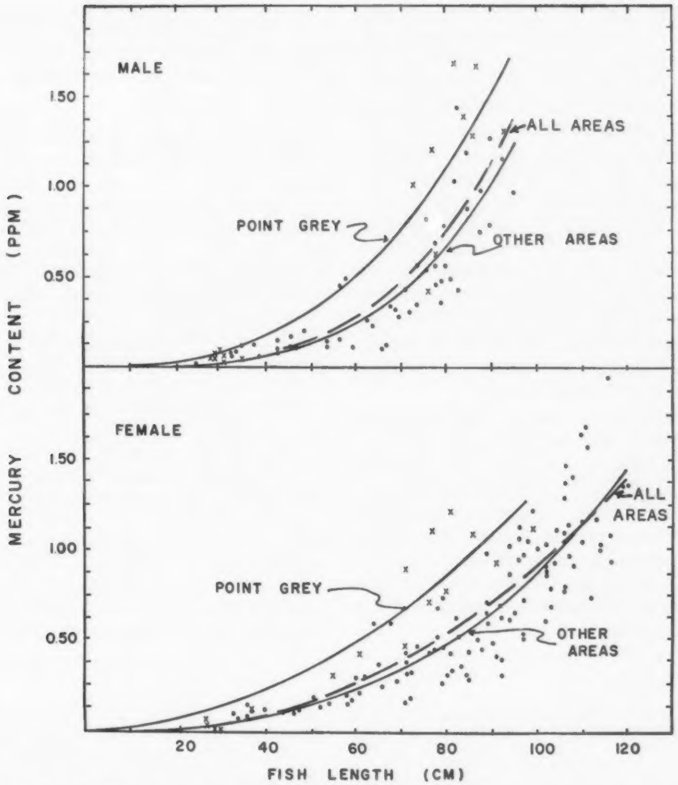

FIG. 2. Relation of total mercury content (*ppm*) to body length, by sex, for dogfish collected in the Strait of Georgia, May–June 1971.

inches). Maximum concentrations observed were 1.68 ppm in males and 1.96 ppm in females.

Analysis of the data by use of normal log likelihood function and chi-square tests was undertaken to determine whether or not (1) a single equation could adequately describe mercury content by length in both male and female dogfish from all areas, and (2) a single equation could adequately describe mercury content by length for males (or females) from all areas.[2] Mercury-length relation was significantly different not only between sexes (as was already evident from gross examination of fish of a given length), but also among areas in both males and females. However, mercury content was not significantly different, for males or females, among areas, if the Point Grey–U.S. Border samples were excluded (Fig. 2). Both male and female dogfish collected in the Point Grey–U.S. Border area contained higher concentrations of mercury for a given length than did dogfish in the other areas. The formulae for the relations are as follows:

Males: Point Grey–U.S.
Border, $y = (727 \times 10^{-8})x^{2.719}$
Other areas, $y = (121 \times 10^{-9})x^{3.538}$
Females: Point Grey–U.S.
Border, $y = (153 \times 10^{-6})x^{1.970}$
Other areas, $y = (370 \times 10^{-8})x^{2.692}$

The reason for the difference in mercury content between males and females is not fully understood. As mercury has been shown to be cumulative with age in some fish species (Johnels et al. 1967), it may reflect a difference in growth rate — males in all probability growing slower beyond a certain age. Reasons for the higher mercury content in dogfish taken in the Point Grey–U.S. Border area are uncertain. However, contamination by effluents from industrial establishments in various places on the Fraser River and estuary may be a contributing factor. The differences in mercury content among areas suggest that dogfish in Georgia Strait are not a homogeneous stock or, if they are, that mercury uptake is very rapid. In United States waters of the Strait and in Puget Sound to the south it was found that 50–65% of tagged dogfish recoveries were made within 20 miles of the tagging area, including those which had been at liberty for up to 6 years (Holland 1957). The same nonmigratory characteristics may be true for the stock in Canadian waters of the Strait, even though extensive movements within the Strait have been noted from tagging (Ketchen unpublished data).

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[2] Because of the limited length range for the sample of males taken in the French Creek-Oyster River area they were deleted from the computations.

The rate of mercury uptake in dogfish is not known. Rapid uptake in trout and young salmon has been demonstrated by Rucker and Amend (1969). If uptake is rapid the extreme variation in mercury content for dogfish of a given length may indicate time spent by various fish in the region of apparent high mercury contamination. On the other hand, there may be large differences in growth rates among individuals, reflecting differences in accumulation with time.

Acknowledgments — Grateful acknowledgment is made to Mr A. Sekerak, who collected the samples, and Mr F. Nash, who programmed the material for IBM 1130 computation and Cal-comp plotting.

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Temperature–Salinity Stress and Mercury Uptake in the Fiddler Crab, *Uca pugilator*

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VERNBERG, W. B., AND J. O'HARA. 1972. Temperature–salinity stress and mercury uptake in the fiddler crab, *Uca pugilator*. J. Fish. Res. Bd. Canada 29: 1491–1494.

Uptake of ^{203}Hg was determined in gill and hepatopancreas tissue from fiddler crabs (*Uca pugilator*) maintained under six temperature–salinity regimes. Although the total mercury was relatively constant under all experimental conditions, the percent of mercury in each of the tissues was markedly different. At higher temperatures the crabs seem able to transport mercury from gill tissue to the hepatopancreas more effectively than at lower temperatures. This could be a factor in the toxicity of mercury to fiddler crabs at low temperature.

VERNBERG, W. B., AND J. O'HARA. 1972. Temperature–salinity stress and mercury uptake in the fiddler crab, *Uca pugilator*. J. Fish. Res. Bd. Canada 29: 1491–1494.

Nous avons déterminé la captation du ^{203}Hg dans le tissu des branchies et de l'hépatopancréas de crabes appelants (*Uca pugilator*) maintenus à six régimes différents de températures–salinités. Quoique le niveau de Hg total des branchies et de l'hépatopancréas demeure relativement constant à tous les régimes, le pourcentage de Hg varie grandement d'un tissu à l'autre. A des températures élevées, les crabes semblent capables d'effectuer le transport de Hg du tissu branchial vers l'hépatopancréas plus efficacement qu'à des températures plus basses. Cette particularité peut avoir une influence sur la toxicité de Hg à l'endroit des crabes à de basses températures.

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IT has been only within the past few years that environmental contamination with mercury has been recognized. Aquatic ecosystems are of particular concern since many animals in these environments concentrate large amounts of mercury rapidly (see reviews of Ackefors et al. 1970, and Friberg 1971). Furthermore, freshwater systems and estuaries receive much of the mercury released from industrial processes.

To assess the effects of possible mercury contamination on estuarine animals, a series of studies has been undertaken using one of the most characteristic animals associated with estuaries along the eastern coast of the United States, the fiddler crab, *Uca pugilator*. Although the effects of low concentration of mercury over long periods of time would be most reflective of the natural exposure of animals to mercury pollution, it was felt that higher, but sublethal, concentrations could give short-term indices of the toxic properties and physiological fate of the metal. It was found that the highest concentration of mercury adults could tolerate for prolonged periods of time (2–3 months) under an optimum temperature–salinity regime (25 C, 30‰) was 0.18 ppm (0.18 mg/liter) (Vernberg and Vernberg 1972a). Under more stressful temperature–salinity regimes, exposure to mercury lessened survival times. For example, under conditions of low salinity (5‰) and high temperature (35 C) both female and male crabs survived at least 1 month with only slight mortality. When 0.18 ppm Hg was added to the water, however, survival times of both males and females were reduced: 50% of the males died by day 17, while 50% of the females died by day 26 (Vernberg and Vernberg 1972a). Under conditions of low temperature and optimal salinity (5 C, 30‰), 50% of the warm-acclimated male crabs died by day 10, while 50% of the females died by day 20. When 0.18 ppm mercury was added the 50% mortality rate for males was reached by day 7, for females by day 14 (Vernberg and Vernberg 1972b). Studies indicated that both gill tissue and hepatopancreas accumulated mercury rapidly under optimum temperature and salinity conditions. The question then arose as to whether or not the observed increased mortality under less than optimal conditions reflected increased mercury uptake in the crab tissues. Accordingly, experiments were designed to assay mercury uptake by gill and hepatopancreas tissues of crabs exposed to various conditions of temperature and salinity.

Materials and methods — Crabs were collected near the Belle W. Baruch Coastal Research Institute field station, Georgetown, S.C. Collections were made in December when air temperature range was 11–21 C. The crabs were brought into the laboratory where they were maintained in plastic boxes, approximately 40 to a box, containing a thin layer of 30‰ sea water. All crabs were maintained in constant temperature boxes at 25 C on a 12L:12D light schedule for a minimum of 2 weeks. Previous studies (Vernberg 1959) have shown that metabolically the crabs acclimate within this time period. Crabs were fed on Clark's fish pellets every other day and the water was changed after each feeding.

After this acclimation period the crabs were exposed to six different temperature–salinity conditions in combination with an initial concentration of 0.18 ppm mercury (0.18 mg Hg^{++}/liter sea water). All crabs were in the intermolt stage and only intermediate-sized crabs (live weight 1.8–2.4 g) were used. Thirty crabs (15 male and 15 female) were placed in 23 × 30 cm boxes under one of the following temperature–salinity regimes: 33, 25, or 5 C in 5‰ or 30‰ sea water. The crabs would encounter these temperatures and salinities in nature. Mercury was added in the form of $HgCl_2$ plus one μCi of ^{203}Hg to bring the initial concentration to 0.18 ppm Hg^{++}. Salinities were adjusted by the addition of distilled water, and 300 ml of water of the desired salinity were added to the boxes. The crabs were maintained on the same light schedule followed during the acclimation period (12L:12D). Mercury concentration did not remain constant but ranged from the initial concentration of 0.18 ppm to a concentration of 0.02–0.05 ppm at the end of the three day experiment.

Groups of six (three male and three female) active animals exposed to each experimental regime were sacrificed after 24, 48, and 72 hr. Gill and hepatopancreas tissues were immediately removed, weighed, digested in 1 ml of Soluene for 24 hr, and then 9 ml of scintillation fluid were added. Concentrations of ^{203}Hg were determined by liquid scintillation on a Packard Tricarb Model 3320 counter. Since each 1.0 μCi represented 0.054 mg of mercury in the test water, a simple ratio of counts per minute to μg of mercury per mg wet weight was determined.

Significant difference of means was calculated by the method of Simpson et al. (1960) for small samples.

Results and discussion — There were no differences between mercury uptake in tissues of male and female crabs. Consequently, the data were pooled. Results are summarized in Table 1.

Gill tissue accumulated much greater amounts of mercury than did the hepatopancreas regardless of the experimental conditions. Over 82% of the mercury accumulation in the gill tissue occurred within the first 24 hr in all thermal–salinity regimes, with only slight additions after 48 and 72-hr exposure to all experimental conditions except 5 C, 5‰. Under a thermal–salinity regime of 5 C, 5‰, the mercury content declined slightly after 72 hr, probably due to necrosis and sloughing of the gill epithelium.

The amount of mercury accumulated in gill tissue within the first 24 hr was significantly higher (at the 1% significance level or less) under the thermal–salinity regime of 5 C, 5‰, than in tissues of crabs maintained in any other set of experimental conditions. Under experimental conditions of 5 C, 30‰, mercury accumulation in gill tissue was significantly greater than at 25 C, 30‰, or at 33 C, 5 or 30‰. The least amount of mercury accumulated in gill tissue of crabs maintained at 33 C, 30 ‰. Under these environmental conditions significantly less mercury accumulated in gill tissue than in any other experimental conditions except 25 C, 30 ‰. Thus, low salinity increased mercury accumulation in gill tissue at all temperatures, and low temperatures further heightened mercury accumulation.

In the hepatopancreas the concentration of mercury increased throughout the 72-hr exposure in all experimental conditions except 5 C, 5 ‰ (Table 1). The amount of mercury accumulated in the hepatopancreas of crabs exposed to 5 C, 5 ‰, for 24 hr was significantly lower than that of crabs maintained under any of the other experimental conditions. After 72 hr less mercury had accumulated in the hepatopancreas of crabs maintained at 5 C in either 5 or 30‰ salinity than in the hepatopancreas of crabs maintained under any of the other experimental regimes. Crabs exposed to 33 C, 30‰, contained 14 times more mercury in the hepatopancreas than crabs exposed to 5 C, 5‰.

The influence of temperature on toxicity of pollutants in animals is not clear. Sprague (1970) stated that "no assumptions should be made about temperature effects on toxicity." Only slight temperature effects have been reported for toxicity of naphthenic acid and zinc to fish (Cairns and Scheier 1957, 1962). On the other hand, there appears to be an inverse correlation between temperature and toxicity with animals exposed to chlorinated hydrocarbons (Elson 1967; Anderson 1968). Fiddler crabs were found to withstand mercury in combination with high temperature and low salinity better than in combination with low temperature and low salinity, although mortalities at both low and high temperatures were greater than under optimum temperature–salinity regimes (Vernberg and Vernberg 1972a).

Although the total mercury in the gills and hepatopancreas, when calculated as μg of metal present in each tissue and added together, was relatively constant for crabs under all the experimental conditions, the experimental regime did influence the distribution of the mercury in these two tissues (Table I). The difference in percent of

TABLE 1. Mercury content in hepatopancreas (H) and gill (G) tissues from fiddler crabs exposed to 0.18 ppm Hg^{++} over a 72-hr period under various temperature–salinity regimes. Values are means of determinations on tissues of 6 crabs ± standard error.

	24 hr			48 hr			72 hr		
Temperature–Salinity Regime	Total μg Hg^{++} in G and H	% in G and H	ppm Hg^{++} in G and H	Total μg Hg^{++} in G and H	% in G and H	ppm Hg^{++} in G and H	Total μg Hg^{++} in G and H	% in G and H	ppm Hg^{++} in G and H
5 C, 5‰	0.46±0.037	H 3.3	0.2±0.03	0.53±0.025	H 6.2	0.3±0.08	0.49±0.028	H 3.7	0.3±0.04
		G 96.7	19.7±1.35		G 93.8	18.9±0.92		G 96.3	15.0±0.80
5 C, 30‰	0.47±0.024	H 11.0	0.8±0.11	0.42±0.038	H 7.2	0.6±0.05	0.42±0.082	H 7.9	0.9±0.15
		G 89.0	14.8±1.53		G 92.8	15.4±1.47		G 92.1	17.1±1.50
25 C, 5‰	0.34±0.061	H 15.2	1.1±0.44	0.46±0.044	H 24.7	1.8±0.53	0.46±0.008	H 31.0	2.4±0.62
		G 84.8	10.5±1.80		G 75.3	12.8±1.39		G 69.0	12.5±0.86
25 C, 30‰	0.38±0.033	H 35.9	2.2±0.80	0.44±0.055	H 40.4	2.5±0.50	0.44±0.072	H 50.9	2.7±0.28
		G 64.1	8.9±0.60		G 59.6	9.0±0.76		G 49.1	10.0±1.09
33 C, 5‰	0.43±0.032	H 35.6	2.1±0.46	0.41±0.060	H 32.5	2.8±0.59	0.46±0.039	H 38.7	2.3±0.70
		G 64.4	10.7±1.11		G 67.5	11.9±2.62		G 61.3	12.0±0.33
33 C, 30‰	0.36±0.059	H 43.8	2.8±0.31	0.45±0.049	H 44.0	3.4±0.58	0.40±0.077	H 64.9	3.6±0.61
		G 56.2	7.2±0.77		G 56.0	8.2±0.66		G 35.1	7.5±0.67

mercury in tissue from crabs exposed to the various thermal–salinity regimes suggests that at higher temperatures the crabs are able to transport mercury from gill tissue to the hepatopancreas more effectively than at low temperatures. For example, after 72 hr the percent of mercury in the gill and hepatopancreas was 35.1 and 64.9, respectively, at 33 C, 30‰, but 96.3 and 3.7 at 5 C, 5‰, and 92.1 and 7.9% at 5 C, 30‰. At low temperatures the crabs are seemingly unable to transport the mercury away from the gills. The inability to transfer mercury from gill tissue to the hepatopancreas at low temperature could be a factor in the toxicity of mercury to fiddler crabs at low temperature.

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Food Availability and Consumption by Young Connecticut River Shad *Alosa sapidissima*[1]

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LEVESQUE, R. C., AND R. J. REED. 1972. Food availability and consumption by young Connecticut River shad *Alosa sapidissima*. J. Fish. Res. Bd. Canada 29: 1495–1499.

Food habits of young American shad (*Alosa sapidissima*) were studied in the Connecticut River above Holyoke, Massachusetts, 1969. Diurnal feeding data revealed a peak in stomach content volume at 8:00 PM during midsummer. Larval shad fed mainly on aquatic crustaceans and tendipedid larvae and pupae. Juveniles ingested the most abundant organisms: crustaceans, tendipedid larvae and pupae, hydropsychid larvae and adult insects. Electivity data indicated positive selection for tendipedid pupae and crustaceans and negative selection for hydropsychid larvae and tendipedid larvae. Selection of Trichoptera larvae by young shad in significant amounts was documented for the initial time.

LEVESQUE, R. C., AND R. J. REED. 1972. Food availability and consumption by young Connecticut River shad *Alosa sapidissima*. J. Fish. Res. Bd. Canada 29: 1495–1499.

Les auteurs ont étudié le régime alimentaire de jeunes aloses savoureuses (*Alosa sapidissima*) de la rivière Connecticut en amont d'Holyoke, Massachusetts, en 1969. Les données recueillies durant le jour à la mi-été révèlent un maximum de volume du contenu stomacal à 2000 h. Les aloses larvaires se nourrissent surtout de crustacés aquatiques et de larves et pupes de tendipédides. Les jeunes se nourrissent des organismes les plus abondants: crustacés, larves et pupes de tendipédides, larves et adultes d'hydropsychides. Les données sur le choix de la nourriture démontrent une sélectivité positive à l'endroit des pupes de tendipédides et des crustacés, et une sélectivité négative vis-à-vis des larves d'hydropsychides et de tendipédides. Le choix de larves de tricoptères par les jeunes aloses est démontré pour la première fois.

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IN 1964, the Massachusetts Cooperative Fishery Unit initiated a long-term study of certain ecological parameters in a 57.3 km section of the Connecticut River between the Holyoke and Turners Falls dams. Several researchers have contributed information on bottom types, benthos, fish composition and distribution, food of selected, fish and life history of the American shad (*Alosa sapidissima*) (reviewed by Levesque MS 1970). Watson's (MS 1968) preliminary food analysis highlighted the need for a detailed investigation.

Our research provides specific data on (1) stomach content of young-of-the-year shad and (2) relationships between stomach content and relative abundance of planktonic and benthic organisms. Although other studies have analyzed food of young shad, only Leim (1924), Mitchell et al. (1925), and Maxfield (1953) related stomach content to food availability. Of these only Mitchell et al. worked on the Connecticut River and his work was below the Holyoke Dam.

Materials and methods — Young-of-the-year shad, plankton, and benthos were collected from June to October, 1969 at three stations on the Connecticut River located at 11.3, 30.7, and 53.3 km above the Holyoke Dam. Beach seines proved best for shad collection. Six fish per sample (two large, two small, and two of medium size) were measured for total length (± 0.1 mm TL) and weighed (± 1.0 mg). Stomach contents were enumerated in a Sedgewick-Rafter counting chamber. Like items were grouped and the percentage of the total volume visually estimated. Dry weight and water displacement techniques were tried but rejected because of the extremely small volumes involved. During July and again in August, 1969, young shad were collected

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at 2-hr intervals to determine feeding chronology. Five stomachs per interval were examined for percentage of fullness. These data were tested in a Kruskal-Wallis one-way analysis of variance by ranks for a difference among the amounts of food present in stomachs.

Plankton was collected at each station with a Clarke-Bumpus plankton sampler (00 size mesh) at a depth of 1–2 m (due to variable water depth) on a back and forth course that extended to mid-stream. The mean volume of water sampled per tow was 5433.7 liters. Analysis of plankton followed a method outlined by Kutkuhn (1958), modified by Miller (1961) and slightly altered for our study. Items were visually assigned volume percentage values. Benthic samples ($0.3m^2$) were obtained with a Peterson dredge.

The presence of a very similar larval type, *Alosa aestivalis*, made larval (less than 28 mm TL) identification difficult. Myomere counts from operculum to anus (Leim 1924), the ratio of body depth to length and dorsolateral pigmentation were used as distinguishing characters.

Ivlev's (1961) "Electivity Index" was employed to assess shad feeding selectivity. E values obtained may range between –1 and +1; the former indicates complete selection against an item (avoidance) and the latter indicates total selection for an item. Indices in this study were restricted to major food items: hydropsychid larvae, tendipedid larvae, tendipedid pupae, and crustaceans.

Results and discussion — (*Feeding chronology*) The 24-hr feeding intensity of larval shad 25.5 mm mean TL (Fig. 1) shows stomach content volume increasing during the July samples up to 7:00 PM. However, no specimens were obtained even with hourly sampling, from 8:00 PM until the 6:00 AM collection. A highly significant difference among the amounts of food present in stomachs during August (mean TL 55.9 mm) was determined by using the ratio of dry stomach with content weight to the fish's wet weight in a Kruskal-Wallis one-way analysis of variance by ranks. Our calculated H value and the tabled value are:

calculated H = 28.57 (10 df)
tabled H = 23.21 (.01 confidence level).

This difference may be the result of increased feeding at 8:00 PM. Our observations agree with Massmann (1963), Walburg and Nichols (1967), and Marcy (1969).

Larval food — Of 147 larvae examined, 94 contained food (Table 1). In fish, 14–21 mm TL, the most abundant (volume) items were cyclopoid copepods (27.8%), tendipedid larvae (24.3%), tendipedid pupae (12.5%), and *Daphnia pulex* (12.3%). Combined crustaceans totaled 57.2% of the stomach content by volume and diptera larvae and pupae accounted for another 36.7%. No larval shad were eaten by this size range of fish. The 21–28 mm fish ingested less cyclopoida (10.0%), more tendipedid larvae (30.7%) and the volume of *D. pulex* eaten remained similar (12.0%). Larger fish ate their own larvae (14.4% by volume), which represents the only major difference between the two size ranges. Shad feeding on their own kind has been described by Mitchell et al. (1925) and Leim (1924). A specimen 14.5 mm TL was the smallest fish with food. Other researchers cited initial feeding at 10.0–15.0 mm (Leim 1924; McDonald 1884).

Juvenile stomach content — Stomach content of 189 juvenile shad was compared with the abundance of organisms in the environment (Table 2). Although phytoplankton appeared in all plankton hauls (86% by volume) and stomachs, its appearance in the stomachs was only in trace amounts and did not constitute a major food source. Tubifex worms occurred in 70.5% of all benthic samples but were not ingested by shad.

We found that five food items dominated (80% by volume) the juvenile stomach content (crustacea, 34%; tendipedid larvae, 15%; tendipedid pupae, 7%; hydropsychid larvae, 13%; and adult insects, 11%). Chi-square tests using the numbers of tendipedid larvae, tendipedid pupae, and hydropsychid larvae between stations indicated that there were no significant differences in the distribution of tendipedid larvae or pupae between stations 30.7 and 53.3 and also the distribution of tendipedid

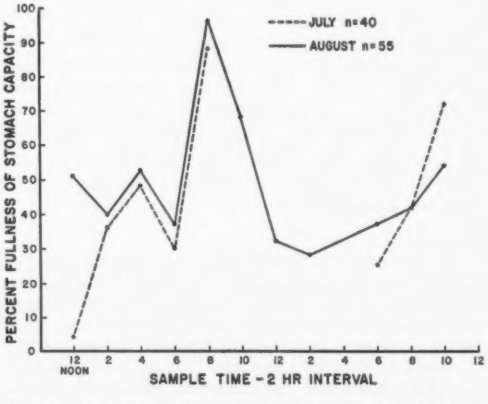

FIG. 1. Diurnal feeding pattern of young shad collected from the Connecticut River, Massachusetts: on July 1 and 2, 1969 at stations 11.3 and 16.1 (mean 25.5 mm TL) and on August 1 and 2, 1969 at station 16.1 (mean 55.9 mm TL)

pupae between the stations at 30.7 and 53.3 km above Holyoke Dam was nonsignificant. All other chi-square data indicated significance between all stations for the three items tested. Because chi-square data indicated that stations were generally dissimilar in their distributions of three of the main food items, we did not combine station data for use as an overall sample.

Our electivity data (Fig. 2) suggest that shad were positively selecting tendipedid pupae and crustaceans at all stations and negatively selecting hydropsychid larvae and tendipedid larvae at all stations except for hydropsychid larvae at station 53.3. A complex bottom type and a daily discharge of impounded water just above station 53.3 may have reduced the accuracy of our hydropsychid larvae data at station 53.3 and affected the electivity index.

Although the data show negative selection for hydropsychid larvae they are still an important food (13% by volume). Ours is the first study to identify these larvae as substantial shad food. Massmann (1963) and Marcy (1969) mention trichopterans as shad food but only as occasional and insignificant.

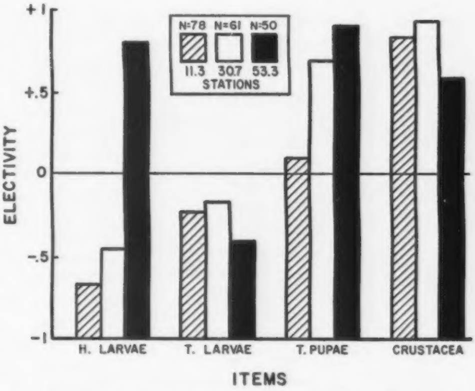

FIG. 2. Electivity indices of four shad food items by stations, 1969, Connecticut River, Massachusetts.

TABLE 1. Larval shad food by size range in mean number of organisms per stomach ($\bar{X}$) and mean percentage of total stomach content volume (%).

	Size range			
	14–21 mm (n=47)		21–28 mm (n=47)	
Items	$\bar{X}$	%	$\bar{X}$	%
Cladocera unidentified	–	–	0.60	4.06
Alona affinis	–	–	0.02	0.21
Bosmina longirostris	0.02	2.13	0.04	0.34
Chydorus sp.	–	–	0.02	0.32
Daphnia pulex	0.28	12.34	0.89	12.04
Diaphanosoma brachyurum	0.06	1.70	0.02	0.21
Holopedium gibberum	0.02	0.21	0.02	0.21
Leptodora kindti	–	–	0.02	0.66
Leydigia quadrangularis	0.02	1.06	0.11	0.55
Moina macrocopa	0.02	1.06	0.21	1.17
Sida crystallina	0.09	4.26	0.38	2.67
Total cladocera	0.51	22.76	2.33	22.33
Copepoda unidentified	–	–	0.94	6.17
immatures	0.04	2.34	–	–
Cyclopoida	0.57	27.77	0.72	10.00
Calanoida	0.09	4.36	0.26	2.13
Total copepoda	0.70	34.47	1.92	18.30
Diptera	–	–	0.02	0.86
Tendipedidae larvae	0.38	24.26	1.51	30.74
Tendipedidae pupae	0.17	12.45	0.26	7.34
Trichoptera	–	–	–	–
Hydropsychidae larvae	–	–	0.02	1.06
Ephemeroptera	–	–	–	–
Heptageniidae nymph	0.06	2.13	0.11	3.40
Larval shad	–	–	0.26	14.36
Invertebrate eggs	0.96	3.94	2.49	1.49
Grand total	2.78	100.0	8.92	100.00

TABLE 2. Percentage occurrence of food items in juvenile shad stomachs compared with their occurrence in the plankton and the benthos

Items	Stomachs	Plankton	Benthos
Phytoplankton	100.0	100.0	–
Ectoprocta statoblasts	15.8	2.1	4.6
Tubifex sp.	–	–	70.5
Arachnida	2.5	–	–
Lebertiidae	–	2.1	4.5
Amphipoda	2.6	–	–
Cladocera	10.5	27.7	–
Bosmina longirostris	9.0	17.0	–
Leydigia quadrangularis	44.4	8.5	–
Daphnia pulex	16.9	42.6	–
Holopedium gibberum	–	2.1	–
Leptodora kindti	6.9	8.5	–
Sida crystallina	39.1	31.9	–
Diaphanosoma brachyurum	0	7.0	–
Total Cladocera	65.6	100.0	
Calanoida	32.8	42.5	–
Cyclopoida	21.8	34.0	–
Total Copepoda	37.0	100.0	
Isopoda	–	–	2.3
Ostracoda	1.6	40.4	–
Insecta	10.6	4.3	–
Larvae	3.2	27.7	2.3
pupae	–	4.3	–
Coleoptera	1.0	–	4.5
Haliplidae larvae	–	–	9.0
Elmidae larvae	0.5	–	–
Diptera	13.8	2.1	2.3
larvae	–	–	6.8
pupae	–	–	2.3
Heleidae larvae	–	–	31.8
Tendipedidae larvae	79.9	19.1	88.6
pupae	59.8	17.0	40.9
Ephemeroptera	3.2	–	–
larvae	–	–	4.5
nymph	1.0	–	–
Baetidae nymph	–	–	9.0
Ephemeridae nymph	–	–	2.3
Ephoron sp.	1.0	–	–
larvae	–	–	9.0
Hexagenia sp.	–	–	2.3
Heptageniidae nymph	3.2	–	9.0
Hemiptera	5.8	–	–
Homoptera	9.5	–	–
Cicadidae	5.3	–	–
Hymenoptera	13.2	–	–
Formicidae	1.0	–	2.3
Lepidoptera	2.6	–	–
Hydropsychidae larvae	50.3	–	61.4
pupae	1.0	–	–
Gastropoda	–	–	2.3
Pelecypoda			2.3
Sample size	189	47	44

Adult insects, an important food in our study, have been reported as shad food by others (Massmann 1963; Davis and Cheek 1966).

We suggest that juvenile shad are essentially opportunistic in their feeding; however, they do appear to select food more from the water column than from the bottom or surface.

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Prediction of Copper Toxicity in Receiving Waters

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WILSON, R. C. H. 1972. Prediction of copper toxicity in receiving waters. J. Fish. Res. Bd. Canada 29: 1500–1502.

The 96-hr LC50 of copper to Atlantic salmon parr in water taken from the Exploits River, Newfoundland, is about 125 μg/liter at a total hardness of 8–10 mg/liter $CaCO_3$ and a total alkalinity of 4 mg/liter. However, the addition of spent sulphite liquor from a pulp mill allowed fish to survive more than 180 μg/liter Cu. Considering the variety of organic compounds which have now been shown to chelate dissolved copper, it is likely that a simple model for the prediction of copper toxicity in waters receiving mine effluent will prove impossible.

WILSON, R. C. H. 1972. Prediction of copper toxicity in receiving waters. J. Fish. Res. Bd. Canada 29: 1500–1502.

La LC50 de 96 h du cuivre pour des tacons de saumon atlantique capturés dans la rivière Exploits, Terre-Neuve, est d'environ 125 μg/litre à une dureté d'eau totale de 8 à 10 mg/litre de $CaCO_3$ et à une alcalinité totale de 4 mg/litre. Cependant, l'addition de liqueur résiduaire de sulfite d'un moulin de pâte à papier permet au poisson de survivre à des concentrations dépassant 180 μg/litre de Cu. Compte tenu de la grande variété de composés organiques chélateurs du Cu en solution, la construction d'un modèle simple pour prédire la toxicité du Cu dans les eaux recevant des effluents de mines s'avèrera sans doute impossible.

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FOR many years, regulatory agencies responsible for the enforcement of water quality standards have been seeking criteria about the effects of mining wastes on receiving waters. In areas where the protection of fish stocks is desirable, one of the most important considerations has been the acute toxicity of very low levels of copper which have generally been reported. The purpose of this note is to report an increase in the amount of copper which can be safely tolerated in some types of water.

Much of the information which has been used to evaluate heavy metal toxicity in Canadian waters is based on the data of Doudoroff and Katz (1953), Lloyd and Herbert (1962), and Sprague (1964). These studies reported, in part, on the effects which environmental variables had on copper toxicity. Lloyd (1965) listed the variables as calcium content (hardness), temperature, dissolved oxygen, and activity rate. To these, the effect of *p*H has sometimes been added, but it has generally been conceded that the most important variable in the toxicity of copper to fish was the mitigating effect of increased water hardness. Out of the total quantity of copper contained in water Lloyd (1965) suggested that only the ionic fraction was toxic. Fish were killed by the formation of an insoluble copper–protein complex at the gill surface, which resulted in the sloughing off of the gill epithelium.

However, there have been several recent studies on the effects of chelation on copper toxicity. The trisodium salt of NTA was found to increase the tolerance of Atlantic salmon (*Salmo salar*) to copper by up to 33 times the lethal threshold (Sprague 1968). Sodium citrate and sodium thiosulphate can also decrease the toxicity of copper by forming complexes (Nishikawa and Tabata 1969), and the chelation of copper by humic acids has been found to cause a proportional reduction in its toxicity at low hardness levels (Wildish et al. MS 1971). Stiff (1971a) stated that support for the theory of ionic copper toxicity could be gained by considering the effect of the bicarbonate equilibrium on copper complexing, meaning that the toxicity would depend on alkalinity rather than on hardness. He also reported (Stiff 1971b) the complexing of copper in natural and polluted water by humic acids, amino acids, and polypeptides. These three classes of organic compounds, which have not usually been considered in models of copper toxicity, were able to complex almost all of the dissolved copper in river water.

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Materials and methods — Three static bioassays, with daily toxicant replenishment, were performed on 2- to 3-year-old wild Atlantic salmon parr in 50-liter tanks containing water taken from the Exploits River above Grand Falls, Newfoundland. The total hardness was 8–10 mg/liter as $CaCO_3$, the total alkalinity was 4 mg/liter, and the test temperature range was 18–21 C. In each experiment, tanks containing copper as the toxicant were tested simultaneously with tanks containing a mixture of copper and spent sulphite liquor (SSL). The 96-hr LC50 for the SSL, which was taken from a digestor at the Price (Nfld.) pulp and paper mill in Grand Falls, has been previously estimated as 2000 ppm (Wilson 1972).

Control tanks throughout the tests contained 17–20 µg/liter Cu, because of the addition of mining effluent to the headwaters of the Exploits River above Grand Falls. The *p*H was between 6.7 and 6.5 in tanks where copper was the only toxicant, but the addition of increasing amounts of SSL caused it to drop as low as 5.0. Test concentrations of copper were verified by atomic absorption spectrophotometry at 324.7 nm, and SSL levels were determined using the modified Pearl-Benson method (Barnes et al. 1963).

Results — The 96-hr LC50 in Exploits River water was estimated to be about 125 µg/liter Cu by the graphic method of Sprague (1969). Sprague (1969) reported that few deaths have occurred after 4 days exposure to copper, and it has been common practice to assume that the 96-hr LC50 for copper is the incipient lethal level (ILL).

The ILL found here contrasts strongly with those based on hardness alone. Lloyd and Herbert (1962) reported an ILL of 27 µg/liter with rainbow trout at a hardness of 10 mg/liter, and Sprague and Ramsay (1965) reported an ILL of 32 µg/liter with Atlantic salmon at a hardness of 14 mg/liter. A large part of the difference between these values and the one reported here could be accounted for by the presence of organic complexing agents in the Exploits River water. The humic acid concentration in stored samples of the test water was determined spectrophotometrically from its absorption at 235 nm (V. Zitko personal communication) to be 4.5–5.0 mg/liter.

The addition of sublethal amounts of SSL to the test water further decreased the toxicity of copper. Results of the tests on mixtures were pooled into a three dimensional graph (Fig. 1), similar in principle to the one used by McLeese (1956). Sublethal concentrations of SSL above 120 ppm permitted at least some of the fish to survive copper concentrations of more than 125 µg/liter. There was no mortality at 180 µg/liter Cu at an SSL concentration of 350 ppm, and even at 250 µg/liter Cu there was only a 10% mortality at 450 ppm SSL.

Conversely, there was no copper level which permitted fish to survive more than the 96-hr LC50 for SSL. We can infer that the death of fish in copper–SSL mixtures was due primarily to copper toxicity alone at sublethal SSL concentrations,

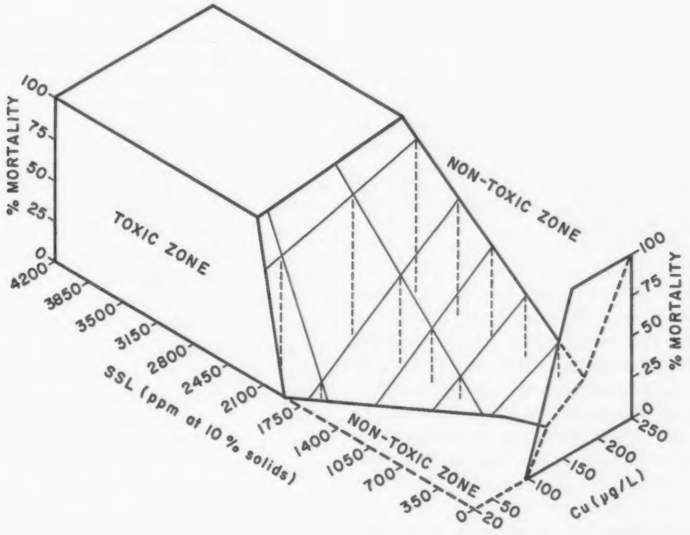

FIG. 1. The response surface defined by the antagonistic effect of SSL on copper toxicity.

although the depressed *p*H at SSL concentrations close to the 96-hr LC50 may have provided additional stress in a few cases. Evidently, at least one fraction of the SSL possesses the capacity to chelate some of the copper ions and remove them from the zone of toxicity.

The chelation of copper by SSL confirms the difficulty of trying to arrive at a simple predictive model for copper toxicity in receiving waters. The number of potential chelators occurring in river water is probably beyond useful definition. There appear to be only two methods available to determine the toxicity of copper in a natural or polluted water: bioassays using the water in question with a copper "spike" added, or the measurement of copper using an ion electrode. While at least one solid state probe is theoretically able to measure copper at the level of one ILL, variations in the total ionic strength of natural waters are an important interference in the measurement of low level dissolved copper solutions by this means. The use of bioassays with the natural water, although more time-consuming, would appear preferable.

Acknowledgments — I thank Dr V. Zitko and Dr R. H. Cook for several interesting discussions on the complexing of copper by humic substances. L. Cole, P. Shallow, and C. Latchem provided help with the bioassay routine and electroseined the experimental fish. Chemical tests were performed by J. Roberts and Dr H. Samant.

This study was conducted as part of the Exploits River Program within the Resource Development Branch, Fisheries Service, Department of the Environment, under the direction of S. G. Pond.

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The Arctic Dredge, a Benthic Biological Sampler for Mixed Boulder and Mud Substrates

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CLARKE, A. H. 1972. The arctic dredge, a benthic biological sampler for mixed boulder and mud substrates. J. Fish. Res. Bd. Canada 29: 1503–1505.

Benthic biological dredges of a new design have been used successfully on ice-rafted archibenthal and abyssal sediments of boulders and mud. The dredge is kite-shaped, of massive construction, and features a single point for cable attachment and a removable cannister for specimen retrieval. Experience in Baffin Bay, the Labrador Sea, and the Icelandic Shelf indicates that the arctic dredge is a reliable tool for arctic and subarctic research.

CLARKE, A. H. 1972. The arctic dredge, a benthic biological sampler for mixed boulder and mud substrates. J. Fish. Res. Bd. Canada 29: 1503–1505.

On s'est servi avec succès de dragues benthiques d'une nouvelle conception pour recueillir des spécimens biologiques dans des sédiments de roches erratiques et de boue transportés par les glaciers dans les zones benthique supérieure et abyssale. En forme de cerf-volant, la drague est compacte et résistante; elle présente un seul point d'attache pour le câble et comporte un récipient métallique amovible pour la récupération des spécimens. Les essais effectués dans la baie Baffin, la mer du Labrador et le plateau islandais indiquent que la drague arctique est un outil extrêmement sûr pour la recherche dans les zones arctique et subarctique.

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FIELD experience in Baffin Bay during 1970 demonstrated that conventional dredges are not satisfactory for collecting archibenthal or abyssal animals from mixed boulder and mud substrates. Drag dredges with rectangular frames are often snagged on boulders and lost. If such dredges are of lightweight construction they are frequently bent or torn even if retrieved. Large rocks also often plug their apertures or damage the specimens within. Grab samplers are frequently prevented from closing by rocks and, if they do close, relatively few animals are usually captured from abyssal depths because most populations there are sparse.

In an effort to circumvent these and other difficulties a new dredge was designed by the writer and fabricated by the Technical Services Division of the National Museums of Canada. In 1971 this "arctic dredge" was used on repeated occasions in Baffin Bay, Labrador Sea and the Iceland Shelf, for qualitative work, and always with complete success, i.e. it was always full of substrate (with specimens) when pulled on board and it was never lost or damaged during use.

An exploded view of the arctic dredge is shown in Fig. 1. The dredge is 1 m wide, 2 m long, 0.2 m high and weighs about 900 lb. The volume of the dredge including the cannister (17.5 liters) is 125 liters. A weak-link device for emergency retrieval (not shown) was always rigged externally but it was never needed. A weak-link will be built into subsequent models of the dredge.

Prior to use, a pinger is attached to the towing cable 50 ft above the dredge so that the location of the dredge may be monitored by use of an electronic depth recorder. A crane is used for shipboard handling. After a dredging operation has been completed the contents are concentrated by washing away the fine sediment through the side screens with sea water using gentle water pressure and fine spray from a hose. When the contents are concentrated sufficiently so that they fill only the cannister, (this operation takes about 1 hr) the cannister and its contents are removed to the laboratory for further examination and processing.

Advantageous design features of the dredge are as follows: (1) The kite-shaped construction and single cable attachment allow the dredge to be deflected around obstructions rather than to be held fast by them; (2) The vertical bars obstruct the entry of rocks larger than three inches in diameter and contribute substantially to structural strength; (3) The heavy construction precludes structural damage during operation and makes the

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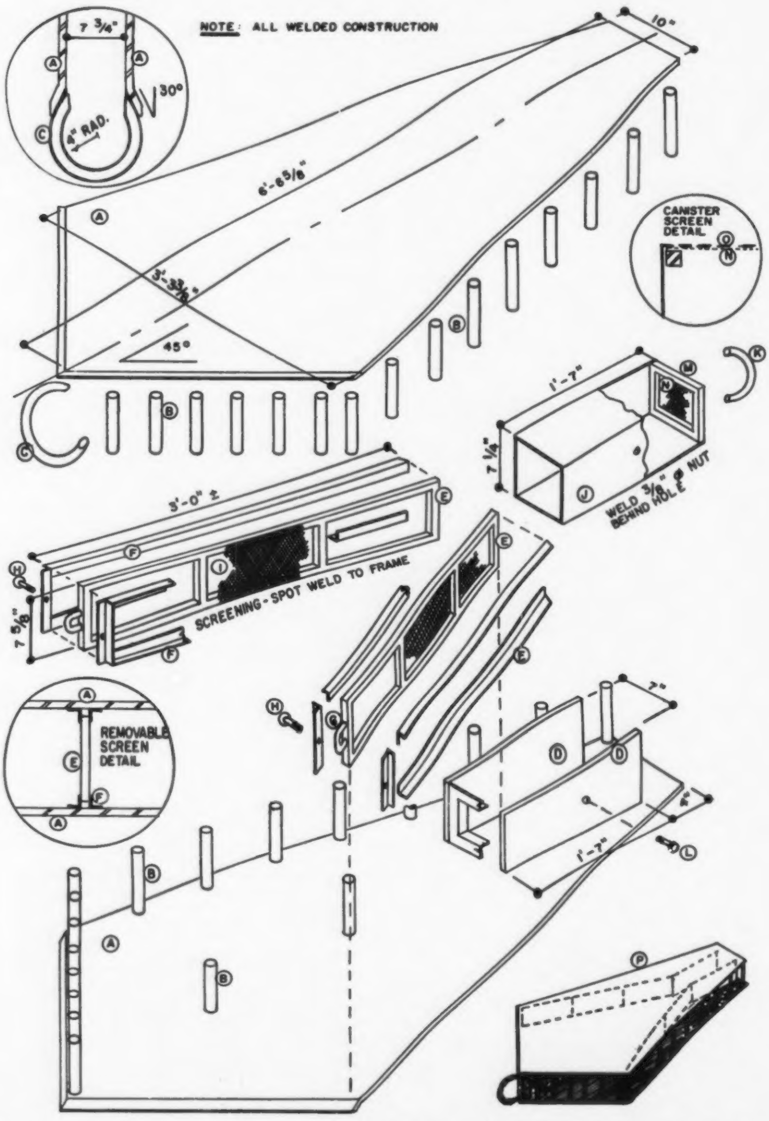
NOTE: ALL WELDED CONSTRUCTION
7 3/4"
A
A
30°
4" RAD.
C
10"
6'-8 5/8"
A
3'-3 3/8"
45°
B
CANISTER SCREEN DETAIL
O
N
1'-7"
M
N
K
C
B
7 1/4"
J
WELD 3/8" ⌀ NUT BEHIND HOLE
3'-0" ±
E
F
H
I
SCREENING - SPOT WELD TO FRAME
7 5/8"
F
E
E
REMOVABLE SCREEN DETAIL
A
E
F
A
H
G
7"
D
D
4"
L
1'-7"
B
A
B
P

FIG. 1. Exploded scale drawing of the arctic dredge. Material throughout is mild steel unless otherwise specified. A, body, ½-inch steel plate; B, support rods, 1-inch diameter rod; C, towing ring, 1-inch diameter rod; D, cannister chamber, ½-inch steel plate, 1- × 1- × ⅛-inch angle, ⅜-inch nut; E, side screen frames, ½- × ½-inch bar; F, slide guides, 1- × 1- × ⅛-inch angle; G, pull ring, ⅜-inch diameter rod; H, hold bolts, ⅜ × 1½ inch; I, side screens, 40 wires to 1 inch (stainless steel); J, cannister, 14 gauge cold rolled steel, ½-inch diameter rod; K, cannister handle, ½-inch diameter rod; L, hold bolt, ⅜ × 1½ inch; M, cannister screen frame, ½- × ½-inch bar; N, cannister screen, 40 wires to 1 inch (stainless steel); O, cannister screen brace, ½-inch 20 gauge flat expanded metal; P, complete unit showing position of side screens and cannister chamber.

addition of supplementary weights for cable depression ordinarily unnecessary; (4) The side screens are removable and can be easily repaired or replaced if punctured; and (5) The removable cannister facilitates transfer of the concentrated dredge contents to the laboratory where further processing can be done more carefully and conveniently than on deck. The latter attribute is especially useful when working in the arctic.

Acknowledgments — I wish to thank the Technical Services Division, NMC, for building the dredge and for preparing the drawing shown here, the Bedford Institute of Oceanography for providing ship-time and facilities aboard C. S. S. *Dawson* and C. S. S. *Hudson*, and the United States Naval Oceanographic Office for ship-time and facilities aboard U.S.N.S. *Lynch*. Special appreciation is also expressed to Mr B. T. Kidd for field assistance and to Mrs M. F. I. Smith and Mrs J. W. Topping for constant help in the laboratory.

The Percent Un-Ionized Ammonia in Aqueous Ammonia Solutions at Different *p*H Levels and Temperatures

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TRUSSELL, R. P. 1972. The percent un-ionized ammoniain aqueous ammonia solutions at different *p*H levels and temperatures. J. Fish. Res. Bd. Canada 29: 1505–1507.

Previous studies have shown that the un-ionized ammonia molecule and not the ammonium ion is the form of the toxicant harmful to fish. Prior attempts to quantify the amount of un-ionized ammonia in an aqueous solution have been confusing. Data given here provide ready access to the amount of un-ionized ammonia over a range of temperature and *p*H that is common in temperate freshwater environments.

TRUSSELL, R. P. 1972. The percent un-ionized ammonia in aqueous ammonia solutions at different *p*H levels and temperatures. J. Fish. Res. Bd. Canada 29: 1505–1507.

Des études antérieures ont démontré que la forme du toxique affectant les poissons est la molécule d'ammoniac non ionisé, et non l'ion ammonium. Les essais effectués dans le passé en vue de déterminer la quantité d'ammoniac non ionisé en solution aqueuse ont prêté à confusion. Les données qui suivent permettent de trouver facilement les quantités d'ammoniac non ionisé dans les intervalles de températures et de *p*H ordinairement observés dans les eaux douces de la zone tempérée.

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AMMONIA is probably one of the most common poisons discharged into rivers and its toxicity has been the subject of many investigations. The toxicity of an aqueous ammonia solution or of an aqueous ammonium salt solution depends mostly on the *p*H value of the water since only the un-ionized molecule (NH_3 as opposed to NH_4) is toxic to fish (Wuhrmann and Woker 1948, Downing and Merkens 1955, Llyod 1961). Toxicity is affected to a lesser extent by temperature, dissolved oxygen concentration, bicarbonate alkalinity, and free carbon dioxide concentration of the water (Lloyd 1961, Lloyd and Herbert 1969, Merkens and Downing 1957).

Although Solorzano (1969) has developed a sensitive analytical technique for measuring the total ammonia nitrogen (as NH_3 plus NH_4) in natural waters, there is no convenient tool for determining the relative amounts of NH_3 and NH_4. Table 1 of Burrows (1964) does show, at three different temperatures and several *p*H's, that for every increase of one *p*H unit there is a tenfold increase in un-ionized ammonia. However, the table was not based on accurate ionization constants for aqueous ammonia and, therefore, it does not contain accurate percentages of un-ionized ammonia for the temperatures and *p*H's indicated (J. W. Elliott personal communication). For example, at *p*H 7.5 and 10 C the percentage un-ionized ammonia in Table

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1 of Burrows (1964) is 1.10; the percentage at the same *p*H and temperature in Table 2 of this paper is 0.59. Similarly, at 6.1 C and *p*H 7.8 and a total ammonia concentration of 0.3 mg/liter only 0.86% or 0.0026 mg/liter would exist as NH_3, not 0.0060 mg/liter as calculated in Burrows (1964).

Accurate ionization constants (Table 1) have been used to calculate, by computer, the percentage of un-ionized ammonia at several temperatures and *p*H's shown in Table 2. Having determined total ammonia by a technique such as Solorzano (1969) or others, one can readily determine from Table 2 the amount of un-ionized ammonia (NH_3). Degrees Fahrenheit have been included for the convenience of many fish culturists in North America.

TABLE 1. Ionization constants used in calculating the percent un-ionized ammonia (NH_3) in aqueous ammonia solutions.[a],[b]

Temp. (*C*)	K_i (*ammonia*)	K_w (*water*)
4	1.480×10^{-5}	1.735×10^{-15}
5	1.490×10^{-5}	1.846×10^{-15}[c]
6	1.500×10^{-5}	2.038×10^{-15}
7	1.515×10^{-5}	2.243×10^{-15}
8	1.530×10^{-5}	2.450×10^{-15}
9	1.550×10^{-5}	2.680×10^{-15}
10	1.570×10^{-5}[c]	2.920×10^{-15}[c]
11	1.582×10^{-5}	3.221×10^{-15}
12	1.595×10^{-5}	3.451×10^{-15}
13	1.610×10^{-5}	3.787×10^{-15}
14	1.630×10^{-5}	4.152×10^{-15}
15	1.652×10^{-5}[c]	4.505×10^{-15}[c]
16	1.660×10^{-5}	4.890×10^{-15}
17	1.673×10^{-5}	5.260×10^{-15}
18	1.690×10^{-5}	5.725×10^{-15}
19	1.700×10^{-5}	6.240×10^{-15}
20	1.710×10^{-5}[c]	6.809×10^{-15}[c]
21	1.733×10^{-5}	7.350×10^{-15}
22	1.750×10^{-5}	7.950×10^{-15}
23	1.765×10^{-5}	8.680×10^{-15}
24	1.780×10^{-5}	9.370×10^{-15}
25	1.810×10^{-5}[c]	1.008×10^{-14}[c]

[a] The ionic equilibrium expressions for aqueous ammonia and water are: (*see opposite*)

←

$$K_i\ (\textit{ammonia}) = \frac{(NH_4)\ (OH)}{(NH_3)}$$

$$K_w\ (\textit{water}) = (H) \times (OH).$$

[b] Water (H_2O) is not included in the above equilibrium expressions as water is practically constant in dilute aqueous solutions. The ionic equilibrium constant of water, K_w, is used to determine the hydroxide concentration (OH).

[c] These values were taken from physical chemistry texts or handbooks (Fleck 1966, Weast et al. 1965–66); the others were obtained by Arrhenius type plots using the known values. Those values obtained by plotting are not exact but represent close approximations to the true values.

TABLE 2. Percentage of un-ionized ammonia in aqueous ammonia solutions at different *p*H's and temperatures.

	(*C*) 5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
pH	(*F*) 41.0	42.8	44.6	46.4	48.2	50.0	51.8	53.6	55.4	57.2	59.0	60.8	62.6	64.4	66.2	68.0	69.8	71.6	73.4	75.2	77.0
6.5	.04	.04	.05	.05	.06	.06	.06	.07	.07	.08	.09	.09	.10	.10	.12	.13	.13	.14	.16	.17	.18
6.6	.05	.05	.06	.06	.07	.07	.08	.09	.09	.10	.10	.12	.13	.13	.15	.16	.17	.18	.20	.21	.22
6.7	.06	.07	.07	.08	.09	.09	.10	.11	.12	.13	.14	.15	.16	.17	.18	.20	.21	.23	.25	.26	.28
6.8	.08	.09	.09	.10	.11	.12	.13	.14	.15	.16	.17	.19	.20	.21	.23	.25	.27	.29	.31	.33	.35
6.9	.10	.11	.12	.13	.14	.15	.16	.17	.19	.20	.22	.23	.25	.27	.29	.32	.34	.36	.39	.42	.44
7.0	.12	.14	.15	.16	.17	.19	.20	.21	.24	.25	.27	.29	.31	.34	.37	.40	.42	.45	.49	.52	.55
7.1	.16	.17	.19	.20	.22	.23	.26	.27	.30	.32	.34	.37	.39	.42	.46	.50	.53	.57	.62	.66	.70
7.2	.20	.22	.23	.25	.27	.29	.32	.34	.37	.40	.43	.46	.50	.53	.58	.63	.67	.71	.77	.83	.88
7.3	.25	.27	.30	.32	.34	.37	.40	.43	.47	.51	.54	.58	.62	.67	.73	.79	.84	.90	.97	1.04	1.10
7.4	.31	.34	.37	.40	.43	.47	.51	.54	.59	.64	.68	.73	.78	.84	.91	.99	1.05	1.13	1.22	1.30	1.38
7.5	.39	.43	.47	.50	.54	.59	.64	.68	.74	.80	.85	.92	.98	1.06	1.15	1.24	1.32	1.42	1.53	1.63	1.73
7.6	.49	.54	.59	.63	.68	.74	.80	.85	.93	1.00	1.07	1.16	1.24	1.33	1.44	1.56	1.66	1.78	1.92	2.05	2.17
7.7	.62	.68	.74	.80	.86	.92	1.01	1.07	1.17	1.26	1.35	1.45	1.55	1.67	1.81	1.96	2.08	2.23	2.41	2.57	2.72
7.8	.78	.85	.93	1.00	1.08	1.16	1.27	1.35	1.46	1.58	1.69	1.82	1.95	2.09	2.26	2.45	2.61	2.79	3.01	3.21	3.39
7.9	.98	1.07	1.16	1.25	1.35	1.46	1.59	1.69	1.83	1.98	2.12	2.29	2.44	2.62	2.83	3.06	3.26	3.48	3.76	4.01	4.24
8.0	1.22	1.34	1.46	1.58	1.70	1.83	1.10	2.12	2.30	2.48	2.65	2.86	3.05	3.28	3.54	3.83	4.07	4.35	4.69	4.99	5.28
8.1	1.54	1.68	1.83	1.98	2.13	2.29	2.50	2.65	2.88	3.11	3.32	3.58	3.81	4.09	4.42	4.77	5.07	5.41	5.83	6.21	6.55
8.2	1.93	2.11	2.29	2.48	2.67	2.86	3.12	3.32	3.59	3.88	4.14	4.46	4.75	5.10	5.50	5.94	6.30	6.72	7.23	7.69	8.11
8.3	2.41	2.64	2.87	3.10	3.33	3.58	3.90	4.14	4.48	4.84	5.16	5.55	5.90	6.33	6.82	7.36	7.80	8.31	8.94	9.49	10.00
8.4	3.02	3.30	3.59	3.87	4.16	4.46	4.87	5.15	5.58	6.01	6.41	6.89	7.32	7.84	8.44	9.09	9.62	10.24	10.99	11.66	12.27
8.5	3.77	4.12	4.47	4.82	5.18	5.55	6.05	6.40	6.92	7.45	7.98	8.52	9.04	9.68	10.40	11.18	11.82	12.56	13.45	14.25	14.97
8.6	4.70	5.13	5.57	5.99	6.44	6.89	7.50	7.93	8.56	9.21	9.79	10.49	11.12	11.88	12.74	13.68	14.44	15.31	16.37	17.30	18.14
8.7	5.85	6.38	6.91	7.43	7.97	8.53	9.26	9.78	10.54	11.32	12.02	12.86	13.61	14.51	15.53	16.63	17.53	18.54	19.77	20.84	21.82
8.8	7.25	7.90	8.54	9.18	9.84	10.50	11.38	12.01	12.92	13.84	14.68	15.67	16.55	17.61	18.30	20.07	21.11	22.27	23.68	24.90	26.00
8.9	8.96	9.74	10.52	11.28	12.07	12.87	13.92	14.66	15.74	16.82	17.80	18.96	19.98	21.20	22.57	24.02	25.19	26.51	28.09	29.44	30.66
9.0	11.02	11.96	12.89	13.80	14.74	15.68	16.91	17.78	19.04	20.30	21.42	22.75	23.91	25.30	26.85	28.47	29.78	31.23	32.96	34.44	35.76

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Recent Articles on FRB Investigations Published in Other Periodicals

Until 1970, reprints of these articles had been included in an annual volume of "Studies," composed of two parts. The final binding was the 1969 Studies, Part 2, which included No. 1355. These are no longer bound and distributed. We continue, however, to number and list all articles, which henceforth may be obtained in reprint form only from the author or originating FRB establishment. The number following each title refers to the FRB establishment listed below.

(1) Fisheries Research Board of Canada
Biological Station
P.O. Drawer 100
Nanaimo, British Columbia

(2) Fisheries Research Board of Canada
Vancouver Laboratory
6640 N.W. Marine Drive
Vancouver 8, British Columbia

(3) Fisheries Research Board of Canada
Pacific Environment Institute
4160 Marine Drive
West Vancouver, British Columbia

(4) Fisheries Research Board of Canada
Freshwater Institute
501 University Crescent
Winnipeg 19, Manitoba

(5) Fisheries Research Board of Canada
Arctic Biological Station
P.O. Box 400
Ste. Anne de Bellevue, Quebec

(6) Fisheries Research Board of Canada
Biological Station
St. Andrews, New Brunswick

(7) Fisheries Research Board of Canada
Marine Ecology Laboratory
Bedford Institute
P.O. Box 1006
Dartmouth, Nova Scotia

(8) Fisheries Research Board of Canada
Halifax Laboratory
P.O. Box 429
Halifax, Nova Scotia

(9) Fisheries Research Board of Canada
Biological Station
St. John's, Newfoundland

1689. Glooschenko, W. A. 1971. The effect of DDT and dieldrin upon ^{14}C uptake by *In situ* phytoplankton in lakes Erie and Ontario. Proc. 14th Conf. Great Lakes Res. p. 219–223. (4)

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1694. Ackman, R. G., S. Epstein, and C. A. Eaton. 1971. Differences in the fatty acid compositions of blubber fats from northwestern Atlantic finwhales (*Balaenoptera physalus*) and harp seals (*Pagophilus groenlandica*). Comp. Biochem. Physiol. 40B: 683–697. (8)

1695. Donaldson, E. M., and Z. H. Shehadeh. 1972. Effect of salmon gonadotropin on ovarian and testicular development in immature grey mullet *Mugil cephalus*, p. 71–85. *In* Z. H. Shehadeh (principal investigator) and K. S. Norris (co-investigator) The grey mullet (*Mugil cephalus* L.): induced breeding and larval rearing research 1970–1972. Publ. Oceanic Inst. Waimanalo Hawaii Rep. No. 01-72-76-1. (2)

1696. Zitko, V., O. Hutzinger, and P. M. K. Choi. 1972. Contamination of the Bay of Fundy — Gulf of Maine area with polychlorinated biphenyls, polychlorinated terphenyls, chlorinated dibenzodioxins, and dibenzofurans. Environ. Health Perspect. 4: 47–50. (6)

1697. Lantz, A. W., and D. G. Iredale. 1972. Canadian Northwest Territories fish and mammal processing plant. Can. Inst. Food Sci. Technol. J. 5(1): A15–A18. (4)

1698. Vaisey, M., M. Slusar, D. Babienko, and A. W. Lantz. 1971. Appraising smoked whitefish with sensory panels, p. 175–180. *In* R. Kreuzer [ed.] Fish inspection and quality control. Fishing News (Books) Limited, London. (4)

1699. Dickie, L. M. 1972. Food chains and fish production. Int. Comm. Northwest Atl. Fish. Spec. Publ. No. 8: 201–221. (7)

1700. Ackman, R. G., S. N. Hooper, S. Epstein, and M. Kelleher. 1972. Wax esters of barracudina lipid: a potential replacement for sperm whale oil. J. Amer. Oil Chem Soc. 49: 378–382. (8)

1701. Gilgan, M. W., and M. E. Zinck. 1972. Estimation of ecdysterone from sulfuric acid induced fluorescence. Steroids 20: 95–104. (8)

1702. Vollenweider, R. A. 1969. Möglichkeiten und Grenzen Elementarer Modelle der Stoffbilanz von Seen. (Possibilities and limits of elementary models concerning the budget of substances in lakes.) Arch. Hydrobiol. 66: 1–36. (In German) (4)

1703. Vollenweider, R. A. [ed.] 1969. A manual on methods for measuring primary production in aquatic environments including a chapter on bacteria. Blackwell Scientific Publications, Oxford and Edinburgh 213 p. (4)

1704. MacFarlane, R. B., W. A. Glooschenko, and R. C. Harriss. 1972. The interaction of light intensity and DDT concentration upon the marine diatom, *Nitzschia delicatissima* cleve. Hydrobiologia 39: 373–382. (4)

1705. Uthe, J. F., F. A. J. Armstrong, and K. C. Tam. 1971. Determination of trace amounts of mercury in fish tissues: results of a North American check sample study. J. Ass. Offic. Anal. Chem. 54: 866–869. (4)

1706. Flannagan, J. F., and G. H. Lawler. 1972. Emergence of caddisflies (Trichoptera) and mayflies (Ephemeroptera) from Heming Lake, Manitoba. Can. Entomol. 104: 173–183. (4)

Additional FRB Publications

The Fisheries Research Board of Canada also publishes a series of *Bulletins*, each on a specific topic. These are for sale by Information Canada, Ottawa, and remittances must be in advance, payable in Canadian funds to the order of the Receiver General of Canada. *Bulletins* are also available from local booksellers and Information Canada bookshops throughout Canada.

The *Annual Report* of the Board and the biennial *Review* of investigations are available free, on request. All publications may be referred to at Board establishments located at: Ottawa; Nanaimo, Vancouver, and West Vancouver, B.C.; Winnipeg, Man.; Ste. Anne de Bellevue, Que.; St. Andrews, N.B.; Halifax and Dartmouth, N.S.; and St. John's, Nfld.

L'Office des recherches sur les pêcheries du Canada publie également une série de *Bulletins*, chacun traitant sur un sujet spécifique. Les publications de l'ORP sont vendues par Information Canada à Ottawa. Les remises, payables d'avance en monnaie canadienne, doivent être établies à l'ordre du Receveur général du Canada. Les *Bulletins* sont aussi en vente chez votre libraire et dans les librairies d'Information Canada.

Vous pouvez obtenir le Rapport Annuel et la Revue biennale gratuitement. On peut consulter ces ouvrages aux établissements de l'Office situés a Ottawa (Ont.) à Nanaimo, à Vancouver, et à Vancouver Ouest (C.-B.), à Winnipeg (Man.), à Ste-Anne-de-Bellevue (P.Q.), à St-Andrews (N.-B.), à Halifax et à Dartmouth (N.-E.), et à St-Jean (T.-N.).

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Board
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Guide to Authors

Details on typing and other items in preparing copy are given in a guide for typists. Also, a list of recommended spellings of about 100 words common in fisheries journals is available from the Office of the Editor.

Editorial Practices

Abstracts should be provided in both English and French.

The *Style Manual for Biological Journals* (2nd ed. American Institute of Biological Sciences, 2000 P St. NW., Washington, D.C.) is, with few exceptions, used as the authority in matters of form. *Webster's Third New International Dictionary* is the standard for spelling and division of words in English; *le Grand Larousse Encyclopédique*, for those in French. Exceptions are made for manuscripts that follow the *Oxford English Dictionary* entirely. Titles of periodicals are abbreviated as in the *Biological Abstracts* list. References to literature are made by the name-and-year system. Manuscript reports are included in the list of references, but are identified both there and in the text by the letters "MS" before the year. The *Journal* follows the spelling recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (Third Edition, 1970), Special Publication No. 6 of the American Fisheries Society.

Notes are distinguished from *papers* on the basis of scope or completeness, rather than quality, of the research. They may be on problems with narrow, readily defined limits; on fishing gear or methods, or research techniques; on advances in knowledge arising as by-products of broader studies; on progress in projects that were discontinued before completion; or on preliminary findings that warrant publication before problems are resolved satisfactorily. Or they may be used to establish priority in publication. They may be organized with as much flexibility as papers except that they may have no centered headings. They should take no more than four pages in the *Journal*.

In general, *series titles* should be avoided.

ILLUSTRATIONS

Line drawings are preferably made with black india ink on white drawing or tracing paper or on coordinate paper with blue grids. All lines, symbols, letters, and numerals must be neat, and legible when the illustration is reduced to the appropriate size. Drawings should be grouped, when feasible, for economy of space. Originals must be submitted and should be less than 20 inches in the greater dimension for full-page illustrations, and proportionately smaller for those taking less than a page. Drawings must not be rolled for mailing.

Prints of photographs should be made on glossy paper with a wide range in tone. They should be cropped, squared, and mounted with rubber cement on white cardboard, with no space between those arranged in groups.

PROOFS AND REPRINTS

Galley proof is sent to the author, and he is responsible for detecting errors in printing as well as in content.

Fifty reprints, without covers, are supplied free. Additional copies needed must be ordered, on the form provided, when the galley proof is returned.

Checklist on Manuscripts

Attention to the following questions will expedite appraisal of manuscripts by referees and editors. The same questions are recommended to referees who review manuscripts for the *Journal*.

GENERAL

Is there new knowledge in the report worth publishing?
  Are the findings, interpretations, and conclusions sound, and relevant to the purpose of the study?
  If the manuscript is merely confirmatory, is it worth publishing?

Does the manuscript need to be rewritten before the work can be assessed?

Is the contribution placed in the proper perspective concerning the state of knowledge of the subject?

Is the manuscript too long?
  Are all the tables and figures needed, and organized for economy of space?
  Would any of the text be clearer if condensed?
  Should some of the data be made available separately, in a manuscript report or at a data repository?
  Should the manuscript be condensed as a Note?

Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

Are summary statements given at the beginnings of sections and paragraphs, and are details in sections and paragraphs relevant to their topics?

Are there inconsistencies between tables or figures and the text, or within the text?

If the manuscript is from a thesis, does it retain characteristics common in these but not desirable in journals?

PARTS OF THE MANUSCRIPT

Does the *title* encompass the content of the report?

Does the *abstract* give the essentials of the new knowledge?

Has the *introduction* all the important guideposts for orienting the reader?

Is review of the literature limited to defining the problem?

Are details of *materials and methods* limited to what scientists need in understanding the design of the study and in judging adequacy of the data obtained?

Are generalizations on the *results* adequate?

Are findings distinguished from inferences from them?

Is *discussion* limited to interpretation and significance of the findings?

If there are loopholes in interpretation, are they acknowledged? Should they be overcome?

Should other interpretations be recognized?

Journal
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Board
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Guide des auteurs

Des détails sur le tapage et certains autres item sont donnés dans le "Guide pour les secrétaires d'auteurs." Aussi, une liste d'épellations recommandées d'environ 100 mots relatifs aux articles sur les pêcheries est disponible au bureau du Directeur de la publication.

Disposition générale

Les résumés doivent être fournis en anglais et en français.

Le *Style Manual for Biological Journals* (deuxième édition, publié par l'American Institute of Biological Sciences, 2000, rue *P* N.-O., Washington, D.C.), a été adopté comme guide des auteurs. Le *Third New International Dictionary* de Webster, dans le cas de l'anglais, et le *Grand Larousse Encyclopédique*, dans le cas du français, font respectivement autorité pour l'orthographe et la séparation des mots. Une exception est faite à l'égard des travaux en anglais qui se conforment entièrement à l'*Oxford English Dictionary*. Les titres de périodiques sont abrégés selon la *Biological Abstracts*. Toute référence à la littérature doit suivre le système nom-année. Les rapports manuscrits sont inclus dans la liste des références, les lettres "MS" avant l'année les identifient dans les références et dans le texte. Le *Journal* se sert des épellations recommandées dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (Troisième édition, 1970), Publication spéciale No 6 de l'American Fisheries Society.

Les *notes* se distinguent des écrits d'après l'étendue de la recherche plutôt que par la qualité de la recherche. Les notes peuvent être sur des travaux de recherche de portée restreinte, susceptibles de découler d'investigations plus considérables, pour la description de techniques de recherche et de méthodes de pêche, pour l'établissement de priorités de publication, et pour faire connaître les renseignements utiles tirés d'entreprises qui ont été interrompues avant d'avoir été achevées. Si la portée de la Note le permet, elle peut être disposée comme un mémoire. D'autre part, la disposition est flexible. La longueur ne doit pas dépasser quatre pages imprimées.

En général, les mémoires en série doivent être évités.

LES ILLUSTRATIONS

Les dessins au trait doivent être exécutés à l'encre de chine sur papier à dessin blanc ou sur papier à calquer, ou sur papier à coordonnées avec quadrillage bleu. Les lignes, les symboles, les lettres et les chiffres doivent tous être propres. Ils doivent être lisibles quand ils sont réduits à la grandeur voulue pour la reproduction désirée. Les dessins doivent être groupés, si la chose est possible, de façon à utiliser tout l'espace disponible. Les originaux doivent être soumis et devraient mesurer moins de 20 pouces dans le sens le plus long pour les illustrations de pages entières, et proportionnellement plus petit pour les illustrations de moins d'une page. Les dessins doivent être postés à plat.

Les épreuves des photographies doivent être tirées sur papier glacé et accuser une gamme étendue de teintes. Elles doivent être coupées, dressées et montées, au moyen de dissolution, sur carton blanc, sans laisser d'espace entre celles qui sont disposées par groupes.

EPREUVES ET TIRES A PART

Les épreuves en placards sont adressées à l'auteur et la responsabilité de toute erreur qui peut y rester lui incombe.

Cinquante tirés à part, sans couverture, sont fournis gratuitement. L'auteur peut profiter du renvoi des épreuves en placards pour commander d'autres tirés à part.

Liste de contrôles pour manuscrits

Une attention particulière portée sur les questions suivantes facilitera l'évaluation des manuscrits par les arbitres et les rédacteurs. Les mêmes questions sont recommandées aux arbitres qui font la critique des livres pour le *Journal*.

GENERALITES

Est-ce que les connaissances nouvelles du rapport méritent d'être publiées?

Les découvertes, les interprétations et les conclusions sont-elles solides et pertinentes au but de l'étude?

Si le manuscrit est tout simplement corroboratif, mérite-t-il d'être publié?

Le manuscrit doit-il être récrit avant d'évaluer le travail?

La contribution est-elle placée dans une perspective appropriée relative à l'état des connaissances du sujet?

Le manuscrit est-il trop long?

Les tables et figures sont-elles toutes nécessaires et arrangées pour économiser le plus d'espace?

Le texte serait-il plus clair s'il était condensé?

Est-ce qu'une partie des données devrait être disponible séparément, soit dans un rapport ou dans un dépôt des données?

Le manuscrit devrait-il être condensé en une note?

Est-ce que la préparation du manuscrit suit la logique mentionnée dans l'introduction?

Y a-t-il des exposés sommaires au début de chaque section et paragraphe, et les détails de ces sections et paragraphes sont-ils pertinents aux sujets?

Y a-t-il des contradictions entre les tableaux et les figures du texte, ou dans le texte même?

Si le manuscrit est tiré d'une thèse, contient-il des caractéristiques communes à cette dernière, mais indésirables dans un journal?

PARTIES DU MANUSCRIT

Le titre renferme-t-il le contenu du rapport?

Le résumé donne-t-il l'essentiel des connaissances nouvelles?

L'introduction a-t-elle tous les points importants afin d'orienter le lecteur?

Le renvoi bibliographique se limite-t-il à la définition du problème?

Les détails du matériel et des méthodes employées sont-ils limités à un minimum pour que les scientifiques comprennent le but de l'étude et puissent porter un jugement adéquat sur les données obtenues.

Les généralisations sur les résultats sont-elles adéquates?

Les conclusions sont-elles déduites des résultats?

La discussion est-elle limitée à l'interprétation et la signification de ces découvertes?

S'il y a des échappatoires dans l'interprétation, sont-elles reconnues? Devraient-elles être maîtrisées?

Devrait-on accepter d'autres interprétations?

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Guide for Typists Preparing Copy

Read the "Guide to Authors" in the current volume of the *Journal*. When in doubt about how to type or arrange details, follow *Journal* practice.

Type the manuscript on white bond paper, not flimsy, preferably size 8.5 × 11 inches (21.5 × 28 cm). If possible, use paper with the lines numbered in the margin. Leave all margins at least 1 inch (2.5 cm) wide. Use a nylon or carbon ribbon and keep the typewriter keys clean.

Double-space all parts of the manuscript, including tables, captions for illustrations, footnotes, and the reference list. Underline only material that is to be printed in italics. Indent the first line of each paragraph in the text and of each footnote.

In titles and headings, capitalize only the first word and proper names and adjectives. For small capitals, use small letters.

Indicate all text footnotes by superscript arabic numbers. Number them consecutively throughout the manuscript, starting with those on the title page. Place each footnote immediately below the reference to it, separating it from the text by horizontal lines.

On the first page type only the title, the authors' names and affiliations, related footnotes, and the running head (Appendix A). Type the abstract on a separate page (Appendix B). Number all pages, beginning with the title page and including those for tables and captions for illustrations.

Have the author check the finished manuscript, and send two copies (the ribbon copy and a carbon copy or a photocopy) to the Office of the Editor.

TABLES

Examine the current volume of the *Journal* to see how tables are set up (Appendix C).

Note especially the following concerning *numbered tables*:

Type each table on a separate page, using paper without the lines numbered.

Number the tables with arabic numerals.

Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra spaces instead.

Indicate table footnotes by superscript small letters and type them below the table.

Place the tables after the list of references.

Where each table is first referred to, type in the margin "Table — near here."

Note that *text tables* are not numbered, they are typed with the text, they seldom need horizontal lines, and the data are arranged in as few rows as possible (Appendix C).

ILLUSTRATIONS

Send the original and two clear copies of each illustration with the manuscript. At the lower left of each figure and copy, give the author's name and the figure number. Also type each caption with its figure for identification. For photographs, type this information on a strip of paper and fasten it to the back of the print. Do not write or type on the print itself. Also, type the captions in succession on a separate page, headed "Captions for illustrations." Put this page at the end of the manuscript.

Where each figure is first referred to, type in the margin "Fig. — near here."

MATHEMATICAL EXPRESSIONS, EQUATIONS, AND FORMULAS

Leave three spaces above and below lines that have much material in superscripts or subscripts, and above and below equations and formulas. In the various expressions, place each component in its correct position (Appendix D).

Show all symbols clearly. In the margin, spell out Greek letters the first time they occur, and distinguish between the small letter l and the numeral one, and between the capital letter O and the numeral zero. Make other explanatory notes similarly.

REFERENCES

Check the text to see that all references in the list are referred to. Type the reference list, double-spaced, in the style that is used in the *Journal* (Appendix E). Names of journals are abbreviated as in the *Biological Abstracts* list, but if an abbreviation is in doubt, type the name in full.

SPELLINGS

A list of about 100 words common in fisheries journals is given in Appendix F.

APPENDICES

Appendices A to F are available on request from the Office of the Editor.

Journal
of the Fisheries
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Guide pour les secrétaires d'auteurs

Lisez le "Guide des auteurs" dans l'édition courante du *Journal*. Si vous avez des doutes sur la façon de taper ou d'arranger les détails, suivez la pratique du *Journal*.

Tapez le manuscrit sur un papier blanc et non un papier pelure, mesurant de préférence 8½ × 11 po. (21.5 × 28 cm) et laissant une marge d'au moins 1 po. (2.5 cm). Si possible, employez un papier avec des lignes numérotées dans la marge. Employez un ruban nylon ou carbone et gardez les clés du dactylo nettes.

Chaque partie du manuscrit doit être tapée à double-interligne au moins. La chose est particulièrement importante dans le cas des tableaux, légendes d'illustrations, renvois au bas de la page et listes de références bibliographiques. Evitez de souligner à moins que la matière ne soit en italique. Mettez en retrait la première ligne de chaque paragraphe du texte, ainsi que de chaque légende et renvoi.

Dans les titres et en-têtes, n'employez la majuscule que pour le premier mot, les noms propres et les adjectifs. Pour les petites majuscules, utilisez les petites lettres.

Indiquez tous les renvois au texte par des chiffres arabes en-tête. Numérotez-les consécutivement à travers le texte en commençant par ceux de la page-titre. Placez chaque renvoi immédiatement sous sa référence, le séparant du texte par des lignes horizontales.

La première page ne doit donner que le titre du sujet, le nom et l'affiliation de l'auteur ou des auteurs, et tout autre renvoi utile (Appendice A). Tapez le résumé sur une page séparée (Appendice B). Numérotez chaque page, débutant avec la page-titre.

Voyez à ce que l'auteur vérifie le manuscrit final, et soumettez la première copie et un double du travail au Directeur de la publication.

TABLEAUX

Consultez une copie du *Journal* pour savoir composer les tableaux et placer les lignes qui y entrent (Appendice C).

Portez une attention particulière à ce qui suit concernant les *tableaux numérotés*.

Tapez les tableaux sur des pages séparées, en utilisant du papier sans lignes numérotées.

Numérotez les tableaux avec des chiffres arabes.

Employez des lignes horizontales au-dessus et au-dessous des en-têtes et au-dessous des colonnes, et très rarement ailleurs. N'employez jamais de lignes verticales; de préférence, laissez de l'espace supplémentaire.

Indiquez les renvois dans les tableaux au moyen de petites lettres italiques en position supérieure et tapez-les au bas de la page.

Placez les tableaux après la liste de références.

A l'endroit où un tableau est mentionné pour la première fois, tapez dans la marge "Tableau (- - -) près d'ici."

Remarquez que les *tableaux dans le texte* ne sont pas numérotés, ils sont tapés avec le texte. Ils ont rarement besoin de lignes horizontales, et l'information est préparée de façons à prendre le moins de rangées possibles.

ILLUSTRATIONS

Joignez au manuscrit expédié le dessin original des illustrations et des photocopies en deux exemplaires.

Au bas et à gauche de chaque figure et photocopie, inscrivez le nom de l'auteur et le numéro de la figure. Aussi, tapez chaque légende avec sa figure pour fin d'identification. Pour les photographies, tapez l'information sur une lisière de papier et collez-la au dos de la photographie. N'écrivez pas et ne tapez pas sur la photographie même. Tapez ensemble sur une feuille séparée et par ordre consécutif les légendes des illustrations, et intercalez cette feuille à la suite du texte.

A l'endroit où chaque figure est mentionnée pour la première fois, tapez dans la marge "Fig. (- - -) près d'ici."

EQUATIONS, FORMULES ET EXPRESSIONS MATHEMATIQUES

Laissez trois espaces au-dessus et au-dessous des lignes qui contiennent du matériel en positions supérieures ou en positions inférieures, et au-dessus et au-dessous d'équations et de formules. Dans les différentes expressions, placez chaque composante dans sa position appropriée (Appendice D).

Indiquez les symboles clairement. Dans la marge, épelez les lettres grecques la première fois qu'elles apparaissent et faites une distinction entre la lettre "l" et le chiffre "un" et entre la majuscule "O" et le chiffre "zéro." Procédez de la même façon pour d'autres notes explicatives.

REFERENCES

Vérifiez le texte afin d'assurer que sont mentionnées toutes les références ou renvois de la liste. Tapez, à doubles interlignes et de la façon prévue (Appendice E) pour le *Journal*, la liste de références. Les noms de journaux sont abrégés suivant la *Biological Abstracts*, mais s'il y a doute, écrivez le nom au long.

VOCABULAIRE

Une liste d'environ cent mots relatifs aux articles sur les pêcheries est disponible au bureau du Directeur de la publication (Appendice F).

APPENDICES

Les appendices de A à F sont disponibles sur demande au bureau du Directeur de la publication.

Bulletin 167 *(Second Editon)*

A Practical Handbook of Seawater Analysis

The original publication on this subject appeared under the title of A Manual of Sea Water Analysis in 1960 as Bulletin No. 125, Fisheries Research Board of Canada. A second edition was published in 1965 and both editions have been long out of print. The first edition of a completely revised and updated version was published under the title of A Practical Handbook of Seawater Analysis in 1968 as Bulletin No. 167, and went out of print in 1971.

This is the second edition of the latter work. It contains revised methods for determination of Ammonia Plus Amino Acids and of Ammonia, and one new method not in the first edition, "Determination of Urea." Minor corrections and alterations have been made throughout the text. These changes will add to the value of this text as an authoritative reference book on seawater analysis.

The senior author, Dr J. D. H. Strickland passed away in California on November 12, 1970. The second author, Dr T. R. Parsons, introduced the changes in this edition.

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Crustacean plankton and the eutrophication of St. Lawrence Great Lakes **K. Patalas** 1451–1462

Notes

Acute zinc toxicity to rainbow trout (*Salmo gairdneri*): confirmation of the hypothesis that death is related to tissue hypoxia **D. T. Burton, A. H. Jones, and J. Cairns Jr.** 1463–1466

Oxidation of lactate to carbon dioxide by rainbow trout (*Salmo gairdneri*) tissues **E. Bilinski and R. E. E. Jonas** 1467–1471

Differences in littoral fauna due to fluctuating water levels below a hydroelectric dam **S. G. Fisher and A. LaVoy** 1472–1476

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Mercury content of spiny dogfish (*Squalus acanthias*) in the Strait of Georgia, British Columbia **C. R. Forrester, K. S. Ketchen, and C. C. Wong** 1487–1490

Temperature–salinity stress and mercury uptake in the fiddler crab, *Uca pugilator* **W. B. Vernberg and J. O'Hara** 1491–1494

Food availability and consumption by young Connecticut River shad *Alosa sapidissima* **R. C. Levesque and R. J. Reed** 1495–1499

Prediction of copper toxicity in receiving waters **R. C. H. Wilson** 1500–1502

The arctic dredge, a benthic biological sampler for mixed boulder and mud substrates **A. H. Clarke** 1503–1505

The percent un-ionized ammonia in aqueous ammonia solutions at different *p*H levels and temperatures **R. P. Trussell** 1505–1507

Recent articles on FRB investigations published in other periodicals 1509–1510
Additional FRB publications 1511
Guides to Authors and Typists *i–vii*

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